ECOLOGICAL ADAPTATIONS OF JAPANESE MACAQUES IN YAKUSHIMA INTO VARIOUS ALTITUDINAL ZONES(Dissertation_全文)

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学位申請論文

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主論文の要旨

「屋久島のニホンザルの異なる標高帯への生態学的適応に関する研究」

屋久島の野生ニホンザルが標高によって異なるさまざまな環境にどのように適応しているかについて、密度と食性を中心にして調査した。まず、山岳地帯で組織的な密度調査を行うため、定点調査と集団追跡を併用した新しい密度調査法を開発し、その有効性を検討した。この方法による推定集団密度は、群れの遊動域の分布から計算される集団密度と一致していたため、この方法は有効であると考えられた。次に、この方法を用いて屋久島西部域の海岸部から山頂部までの相対集団密度の変異を調査した。密度は標高400mまでの海岸部だけがほかよりも高く、それ以上の標高帯では差がなかった。この要因の原因を検討するため、食物樹種の密度、単位面積あたりの食物種数、果実が利用できない期間の長さ、年間の総果実生産量を標高によって比較した。サルの密度変化ともっとも対応していたのは年間の総果実生産量であった。屋久島のニホンザルは果実のない時期に成熟葉を採食するが、これでは一日の必要エネルギーを完全には満足できず、果実の多い時期に蓄えた脂肪を消費しなければならない。果実生産量は、果実の多い時期だけではなく、少ない時期にも脂肪蓄積を通じて屋久島のニホンザルの密度を制限していると考えられた。最後に、糞分析法を用いて海岸部から標高1200mまでの地域の食性を2年間にわたって調査した。食性は標高によって連続的に変異し、標高が低いと種子・果実、昆虫を多く採食し、標高が高いと繊維性食物、キノコを多く採食した。どの標高帯でも食性に季節変化があり、9月から11月にかけてもっとも種子・果実を多く採食し、2月から4月にかけて繊維性食物をもっとも多く採食した。このような変化は果実生産と種子・果実食物種の多様性の変化に対応していると考えられた。

Ecological Adaptations of Japanese Macaques in Yakushima into Various Altitudinal Zones

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Chapter 1. INTRODUCTION

Japanese macaque (*Macaca fuscata*) is one of the few species which have radiated into temperate regions. Temperate region is a marginal habitat for primates, considering most of the extant primates inhabit in the tropics. Ecological adaptations of Japanese macaques in temperate regions would reveal the potential of adaptability primates ever have.

Recently, comparative studies of basic ecological characteristics of primates among communities or continents have increased, and revealed important characteristics on primate community structure in the tropical forest (Fleagle et al, 1999). Studies on Japanese macaques may offer a new perspective on these topics by comparison between temperate and tropical forest.

Basic ecological information, such as diet, density, or habitat is indispensable for studying the species' ecological adaptations, however, studies on these characters have been rarely conducted in Japanese macaques. For example, systematic description of the diet for more than one year is found only in Hill (1997), and there has been no study on the density using systematic census techniques. Information on phenological changes of food resource is also largely lacking, although seasonality is suggested to be the principal character of temperate regions considering its strong abiotic seasonality, such as temperature and day length.

In this study, I present data on density, diet, and habitat of Japanese macaques in Yakushima. Yakushima is an ideal site for ecological comparison, as within-population variation in habitat is expected to be the largest for this species. In Yakushima, Japanese macaques are continuously distributed from coastal warm-temperate broad-leaved evergreen forest to subalpine summit (Yoshihiro et al., 1999). The lowland forest is the richest habitat for this species in terms of food productivity and climate (Maruhashi, 1980). On the other hand, the summit may be

climatically similar to the northern limit of the species distribution (Eguchi, 1984).

This thesis is composed of five chapters. First, I present general introduction of the habitat in Yakushima (Chapter 2). Second, I examine the reliability of a new method to census of Japanese macaques in mountainous habitat (Chapter 3). The steep terrain of habitats inhabited by Japanese macaques have prevented to conduct systematic census, thus this new method is expected to be a methodological breakthrough. Thirdly, using this new method, I study the altitudinal variation of density of Japanese macaques in Yakushima (Chapter 4). The determinants of the variation are explored by comparisons of habitat variables. Lastly, I focus on altitudinal variation in the diet in relation to the variation in fruiting phenology and productivity (Chapter 5).

Chapter 2. STUDY SITE

Yakushima Island is located in the southwest part of Japan (30° N, 131° E), and occupies an area of 503km^2, with the highest peak being 1,935m a.s.l. Mean annual precipitation ranges from 2,500 mm to 4,700 mm along the coast, and it exceeds 8,600 mm in the upper area (Eguchi, 1984). In the coastal area, the mean annual temperature is 20° C, and mean temperature of the coldest month (February) is 11° C (Tagawa, 1980). Japanese macaques and sika deer (*Cervus nippon* Temminck) are the only large mammals inhabiting this island.

Kimura & Yoda (1984) classified the vegetation with altitude into five zones. (1) Subtropical-warm temperate transitional zone (0-99m a.s.l.): subtropical plants such as strangler figs (*Ficus superba* and *F. microcarpa*) are mixed with warm temperate evergreen broad-leaved trees. (2) Warm-temperate evergreen broad-leaved forest zone (100-799m a.s.l.): warm-temperate evergreen broad-leaved trees (e.g., *Castanopsis cuspidata*, *Quercus salicina* and *Distylium racemosum*) are predominant. (3) Warm-temperate/cool-temperate transitional forest zone (800-1,199m a.s.l.): warm-temperate evergreen broad-leaved trees such as *Quercus acuta*, *Quercus salicina*, *Distylium racemosum*, and conifers such as *Cryptomeria japonica*, *Abies firma*, and *Tsuga sieboldii* are mixed. (4) Cool temperate zone (1200-1699m a.s.l.): Conifers such as *Cryptomeria japonica*, *Abies firma*, and *Tsuga sieboldii* are dominant. (5) Summit dwarf scrub (1700m-): tall trees cannot grow, and bamboo, *Pseudosasa owatarii*, cover the summit.

Chapter 3: CENSUS METHOD

Introduction

Line transect census is usually used to estimate group and/or population density of diurnal primates (Defler & Pintor, 1985; Brockelman & Ali, 1987; Whitesides et al., 1988, Lahm et al., 1998; Johnson & Overdorff, 1999; Mitani, Struhsaker & Lwanga, 2000; Fashing & Cords, 2000; Brugiere & Fleury, 2000). In this method, researchers walk along a long straight transect and record the distance from the transect to groups (or nests, individuals, etc.) observed. Group density is calculated by estimating the detectability function in relation to transect-group distance (Buckland et al., 1993). However, this method is not applicable to populations in mountainous habitats, which are too steep to set up long straight transects. For example, Japanese macaques as well as other macaques in temperate regions, have never been censused by a line transect (Oi et al., 1994). Most of the density data on Japanese macaques have been derived from intensive studies (e.g. Takasaki, 1981).

Point census is often used in ornithological studies (Buckland, 1987). Unlike line transect census, it is feasible even if the terrain is steep. The census of gibbons (*Hylobates pileatus*) in Thailand (Brockelman & Srikosamatara, 1993) and tarsiers (*Tarsius spectrum*) in Indonesia (Gursky, 1998) are among the few examples of point census applied to primates. Data were analyzed in a different way from line transect census. In the gibbon census, each group could be identified by the character of loud songs. Group density was calculated by dividing the cumulative number of groups identified at the point by the range area where the point observer was able to hear loud songs. In the tarsier census, Gursky (1998) established a 1 ha grid and checked whether or not a group was in the grid. However, these two methods are not applicable to most of the diurnal primates because usually (1) primate groups cannot be identified by vocal characteristics, and (2) group density is too low to collect enough

data with small grids such as 1-ha.

It is possible to estimate density by point census in the same way as line transect census as long as group-point distance is measured precisely (Buckland et al., 1993). When point census is applied to primates, researchers often have to depend on not only visual but also auditory cues because of the low density and poor visibility. However, it is difficult to record the distance precisely when groups are detected by auditory cues. We devised a new method by combining point census and group follows to measure point-group distance precisely. We used this method on Japanese macaques in Yakushima. Group density was also estimated by home range data to examine the reliability of our new method.

Methods

PROCEDURE OF THE CENSUS

We regard a group as a cluster of macaques that are within 500 m of each other. However, macaques who live in different social units (troops, hereafter) are not regarded as the same group even when they are within 500 m. These cases should be treated as two different groups that are in close proximity ('approach', hereafter).

We established a 7 km^2 census area in the western area of Yakushima. The altitude of the census area is 700-1300 m above sea level. The vegetation is the transitional forest between a coniferous forest and a warm-temperate broad-leaved evergreen forest (Kimura & Yoda, 1984; chapter 2). About two-thirds of the census area was logged 5-15 years ago.

The basic design of our census is the same as that of Oi et al. (1994). To sample the research area evenly, we divided the census area into twenty-eight 500×500 m quadrates (Fig. 3-1). Observers were positioned in each quadrate at a fixed point where they could get a good view over the quadrate. All of the points were on ridges, sometimes at peaks. All of the observers were inexperienced, and they were trained

for one day preceding the census. In this study, 28 observers simultaneously searched for macaque groups visually and auditorially from 6:00-7:00 to around 15:00-16:00. In addition, fourteen experienced researchers followed groups that appeared in the census area whenever possible. They recorded the location of the center of the group at least every hour. Point observers and group followers communicated with each other by walkie-talkies. We carried out the census for six days from August 2 to 7, 2000. On August 2 and 3, we sampled only 16 and eight points, respectively, because some points were not accessible due to the swelling of a river. It did not rain and the wind was not strong during the census. During the census, only four troops were successfully followed (Fig. 3-1). Most of the range of these troops was disturbed by logging activities. The exact group size was unknown except for the HR troop (25). However, all of the troops appeared to be less than 30 in size. The HR troop was totally habituated. The PE and SY troops were partially habituated. The OM troop was very shy toward observers. These four troops were followed for 144 hours in total.

At each point, we counted the number of groups detected in each hour (6:00-6:59, 7:00-7:59, etc) as follows. We considered that a group was detected when a point observer saw any adult female or juvenile or heard vocalizations of several macaques. Observations of adult males or vocalizations of a single animal were not treated as detection of a group. This is justified because all-male groups are rarely found in Yakushima especially in non-mating seasons (Sprague et al., 1998). Two groups would have been counted when a single observer heard vocalizations simultaneously from two places which are more than 500 m apart, although this did not occur during the census.

The number of groups detected each hour was averaged for each day and each point. This value, n, refers to as the number of groups detected in the following analysis. When the point was censused for less than 6 hours, the point's data on the

day was discarded.

MODEL

We estimated group density D from the number of groups detected at each point n with the following model.

Suppose that y is the distance from a point, and $g(y)$ is detectability or the probability at which a group at distance y is detected by the point observer in an hour. Then, N, the expected number of groups detected at the point, is given as follows (Buckland et al., 1993):

$$N = 2D\pi\int_0^\infty yg(y)dy \quad \text{------(eqn 1)}$$

We applied the half-normal model (Buckland et al., 1993), so that $g(y) = e^{-\lambda y^2}$ Then D is calculated by transforming eqn 1:

$$D = \frac{\lambda N}{\pi} \quad \text{------(eqn 2)}$$

N, the expected number of groups detected, is not the same as n, the actually counted number. It is because when two groups that belong to different troops approach (stay closer together than 500 m), point observers count them as one group. Suppose B is the frequency of approach, then

$$N = n(1+B) \quad \text{------(eqn 3)}$$

B is proportional to group density D (Sugiura et al., 2000), thus

$$B = bD \quad \text{------(eqn 4)}$$

where b is a constant. From eqns 2, 3 and 4,

$$D = \frac{\lambda n}{\pi - b\lambda n} \quad \text{------(eqn 5)}$$

$$b = \frac{\pi B}{(1+B)\lambda n} \quad \text{------(eqn 6)}$$

Therefore, two parameters are necessary to estimate D from n. One is λ, which can be calculated by regressing the relationships between distance and detectability on the half-normal model. λ is referred to as 'detectability constant' hereafter. The other is b, which can be calculated from B, the frequency of approach, by eqn 6.

The two parameters can be calculated from the data of group follows. Distances between the groups and all points within 1.1 km from the group were recorded at 50 m intervals every hour. By checking whether the point observers detected the group in the hour, we estimated $g(y)$. Frequency of approach B was also estimated from group follows.

Results

CALCULATION OF PARAMETERS

Detectability rapidly decreased with point-group distance (Fig. 3-2a). A total of 1392 group-point distance data were recorded, and groups were detected by 117 points/hour. The maximum distance at which a group was detected was 550 m. Buckland et al. (1993) recommended truncating the large-distance observations because those data do not contribute to estimating $g(y)$, only to increasing error. Thus, we truncated 10% of the largest-distance detection data in the following analysis. The truncated data closely correlated with the half-normal model (R^2=0.964), with an estimated $\lambda = 30.6$ (Fig. 3-2b).

Detectability did not appear to be affected by the troop identity or topography but by the time of day (Table 3-1a-e). There were no significant differences in the detectability constant among different troops or topographic factors (distance from nearest ridges or rivers, and the difference between maximum and minimum altitude of the 500×500 m quadrate). On the other hand, the detectability constant during early morning (6:00-9:00) was significantly or nearly significantly smaller (thus detectability

was better) than during late morning (9:00-12:00) or afternoon (12:00-). We discarded data when the point was not sampled for more than six hours. Thus, it would be justified to neglect the effect of time of day and use the same detectability constant (30.6) in estimating the group density.

As the point observers were inexperienced, we would expect detectability to improve with greater experience. Comparisons of detectability among the first, second, and last two days were in accord with this expectation (Table 3-1f), but the difference was not significant.

During 144-hour group follows, group approach occurred seven times. In all cases, groups approached one of the four troops. Thus, B is calculated as 7/144=0.0486 (times/hour) in the range of these four troops. Mean n in the range of the four troops (10~16M, 10~16N, see Fig. 3-1) was 0.164, thus b is calculated to be 0.0290 from eqn 6.

ESTIMATING GROUP DENSITY

The number of groups detected at each point, n, averaged over four- or six-day-census period, ranged from 0.00 to 0.38 (Fig. 3-3a).

By substituting λ=30.6 and b=0.0290 into eqn 5, we obtain

$$D = \frac{30.6n}{\pi - 0.887n} \quad \text{------(eqn 5}' \text{)}$$

The variation in estimated group density among points calculated from eqn 5' did not differ significantly from normal distribution (Fig. 3-3b; Kolmogorov-Smirnov test, n=28, D=0.14, p>0.1). The 95% confidence limit of estimated group density in the census area was calculated to be 1.45 ± 0.41 groups/km^2

To examine the reliability of our method, we also estimated group density by home range data of the identified troops in the census area (Fig. 3-1). Complete home range data of neighboring troops are available only for the OM troop. The exclusive

home range of the OM troop was 0.478 km^2 The overlapped home range with the PE troop was 0.066 km^2, and that with the SY troop was 0.078 km^2 By Whitesides et al.'s method (1988), troop density in the home range of the OM troop was calculated as $1/\{0.478+(0.066+0.078)/2\}=1.82$ troops/km^2 The frequency of subgrouping in the census area during census period was 5/144. Therefore, group density was calculated as $1.82\times(1+5/144)=1.88$ groups/km^2 Six points (12-14M, 12-14N, see Fig. 3-1) were within the home range of the OM troop. Group density using the data of these points was calculated as 1.96 ± 0.63 groups/km^2, of which the 95% confidence limit includes the density calculated by home range data.

OPTIMUM CENSUS DURATION

How long a census period is necessary to estimate group density reliably? Although the variance decreases with sample size, the relationship is not linear. There is often an optimum number of sample sizes above which an increase in sample size is not matched by a corresponding decrease in variance (Lahm et al., 1998).

We estimated group density with three parameters: number of groups detected at a point (n), detectability (λ), and frequency of approach (B). B was calculated by limited data, so we examined the other two parameters. To obtain optimum census duration, we examined the change in 95% confidence limits of n and λ with the duration of census days. Examination of n was confined to the 13 points that were sampled for the entire six days.

Fig. 3-4a shows that using data of the first day produced a very wide confidence limit of n. The confidence limit became much narrower by using the data of the first two days, or 27 detections. By using the first three or more days, or more than 50 detections, the width of the confidence limit does not change so much. Therefore, three days would be enough to reliably estimate the number of groups detected in the present case.

Changes in the confidence limit of the detectability constant became stable on the fifth day, or 90 detections of followed groups and 120 hours of group follows (Fig. 3-4b). Therefore, five days would be enough to estimate detectability reliably.

Discussion

Group density of Japanese macaques was reliably estimated by the method of combining point census and group follows. The 'true' density calculated by home range data was within the 95% confidence limit of density calculated by our model. We discuss the assumptions, robustness, and applicability of our new method.

ASSUMPTIONS

There are four fundamental assumptions in point and line transect census (Brockelman & Ali, 1987; Buckland, 1993): (1) Animals near the point or transect are always detected, thus $g(0)=1$; (2) Distance is recorded precisely; (3) Each detection is independent; (4) Locations of animals are not influenced by the observers.

Does our census method satisfy these assumptions?

The first assumption seems to be satisfied by our method as evidenced by the fact that the detectability at the shortest distance (<50m) was close to one (0.905). The second assumption was also satisfied because we located groups by following them. The third assumption would have been violated if we treated the detection data of consecutive hours as different analysis units. The last assumption is difficult to test, but the fact that the detectability of the OM troop, very shy to observers, did not differ from that of other troops suggests that observers did not influence groups so much. Thus, all of the fundamental assumptions of the point census seemed to be satisfied in our method.

One of the differences of our model from the 'typical' point census is that we corrected data with frequency of approach, B. We assumed that $b=B/D$ is a constant,

however, frequency of approach, or encounter, is proportional not only to density but also to ranging speed and group spread (Sugiura et al., 2000). We neglected other factors simply because data were not available to quantify the effects. This may partly be justified because the correction by frequency of approach was not great compared to $g(y)$ (see eqn 5′), so it did not influence the estimate very much.

ROBUSTNESS OF DETECTABILITY

We have shown that the detectability function of $g(y)$ was robust, and not biased with troop, topography or increasing experience of observers. This is important because we could not record the point-group distance in all cases of detection. The robustness of detectability guarantees an estimate of density with the same parameter. Only time of day influenced detectability, but we can control this effect by sampling for an entire day.

Robustness of detectability against topographic factors is important because this method was devised to conduct a census even in steep mountains, where line transect is not possible. Topography, especially distance from nearest ridges, did not affect detectability in our census, although even loud songs of gibbons were assumed not to be transmitted beyond ridges (Brockelman & Srikosamatara, 1993). Among the 139 cases when point-group distance was less than 250 m, there was a ridge between the point and the group in only three cases. Distance was 200 m in all these three cases. Detectability was low at distances where ridges were often found between points and groups (e.g. at 250-500m, ridges were found in 156/194 cases). Detection data of long distances did not influence the estimate of detectability because we truncated large-distance data to avoid errors. This is the most likely reason why the existence of ridges did not influence the estimate of detectability.

Although we did not find any bias in detectability with troops, the effect of group size remains unknown, as the variation in size was small among the four troops.

Therefore, when there is a large variation in group size among the censused population, the effect of group size on detectability should be examined before application of the method.

When censusing many points simultaneously, researchers often have to use inexperienced observers. The effect of increased experience on detectability, if any, was small. We did not regard it as evidence of group detection when the observer heard vocalizations of single animals. Detections by 'apparent' cues, such as exchange of vocalizations, may not need so much experience. Robustness against experience allows us to use inexperienced point observers.

APPLICABILITY

Compared to the line transect census, the advantages of this method are: (1) It is applicable to populations in steep habitats as long as one group can be followed in the census area; and (2) This method enables us to study habitat use by animals at a finer-grained scale. For example, the vegetation of a 500×500 m quadrate and the estimated density of the points in the quadrate are comparable. For this purpose, the number of groups detected at the point, such as that shown in Fig. 3-3a, can be used as relative group density. Considering the robust nature of detectability, it is unlikely that the number of detected groups is biased. The disadvantage is that greater census efforts are required. Gathering 28 observers (even inexperienced) would not be an easy task, or it would take 28 times longer time for a single point observer to collect as many data as by 28 observers. Moreover, group followers are required.

In the present census area, at least two or three days were required to reliably estimate the number of groups detected, and five days to estimate the detectability, by sampling 28 points simultaneously. However, this optimum period would change with population or census design, such as the number of points or the area of quadrates, etc. Alternatively, we recommend repeating the census until the number of group detections

becomes more than 50, and the number of detections of followed groups becomes more than 90 (Fig. 3-4a). We censused 28 points simultaneously, but this is not necessary. It is feasible to census each point on different days.

Our definition of a "group" seems to reflect the normal group spread of Yakushima macaques (Sugiura et al., 2000), but such a definition should be modified for each species. Although we did not estimate the population density, it can be calculated as the product of the group density and the mean group size. The group size would be obtained by group counts taken during group follows.

Chapter 4: VARIATIONS IN DENSITY

Introduction

What determines the density of animal populations? Wolff (1997) suggested the importance of extrinsic factors as determinants of mammalian population density, for example, regulation by predation (Murray, 1999; Isbell, 1990), disease (Milton, 1996), inter-specific competition (Peres & Dolman, 2000), or past catastrophic events (Butynski, 1990; Takatsuki, Suzuki & Suzuki 1994). On the other hand, availability of food resources is suggested to be the principal determinants of mammalian population density by continent-wide interspecific comparisons (Neotropics: Robinson & Redford, 1986; Africa: Fa & Purvis, 1997). It was found that densities of larger-sized, dietary specialized, or higher-trophic-leveled species were low because these species require larger home range to secure more foods. In contrast, the densities of generalists or primary consumers tended to be high.

At the population level, however, evidence on the relationship between food resource and density is largely confined to small mammals (Wolff, 1996; Adler, 1998; Chaquenot & Ruscoe, 2000). In case of large mammals, many studies reported variations in density among habitats, however, most of them failed to quantify the food abundance in each habitat (Takasaki, 1981; Wahlstrom & Kjellander, 1995; Rose & Polis, 1998). Exceptionally, Balcomb, Chapman & Wrangham (2000) showed that the density of trees bearing large fleshy fruits could predict the density of chimpanzees in Kibale, Uganda. Availability of food resource changes over time, however, the importance of temporal scale remains largely unanswered (Janson & Chapman, 1999): Are animal densities regulated by annual total resource, or resources available in seasonal bottleneck, or in ecological crunches (Cant, 1980) which happens once per several years?

Japanese macaques are generalist primates and their diet varies seasonally

(Hill, 1997). They eat young leaves in spring, fruits, insects or mature leaves in summer and fruit and/or seeds in autumn. In winter, when high-quality foods are exhausted, they switch to low-quality diet, such as mature leaves in evergreen forest or buds or barks in deciduous forest (evergreen; Agetsuma, 1995: deciduous; Nakagawa, 1989). Because only high-quality food categories can satisfy their daily nutrient requirements (Nakagawa et al., 1996), winter is a lean period for them. They deposit fat in autumn by eating high-quality fruits and seeds to survive lean winter (Mori, 1979; Watanuki & Nakayama, 1993).

We report the within-population variation of relative group density of Japanese macaques in Yakushima. Although preliminary results of the census have already been reported by Yoshihiro et al. (1999), we completely re-analyzed using systematic procedures. They are ideal subjects of resource limitation because of the following reasons: (1) Their habitat is highly variable with altitude. (2) The effect of seasonality could be detected as habitats and diets are highly seasonal. (3) Many factors other than food are excluded as determinants of density. For example, there is no natural predator or sympatric primate for them. They have been studied since 1975, and no island-wide plague or catastrophe has been known by the time we conducted census.

We describe four habitat variables: (*A*) total basal area of food trees, (*B*) number of food tree species per unit area, (*C*) seasonal fruit abundance, and (*D*) total annual fleshy fruit production. We examine the following hypotheses on the determinant of macaques' density using the variables indicated in the parentheses.

1. Density is determined by the availability of high quality food (*A*).
2. Density is high where diversity of food species is high (*B*).
3. Density is determined by the severity of bottleneck period, the season when the availability of high-quality food is the lowest (*C*).
4. Density is determined by the total annual production of high quality food (*D*).

Hypothesis 1 is expected because nutritional requirement of Japanese macaques is satisfied only by high quality fruits and seeds. Hypothesis 4 is the more rigorous test of hypothesis 1. Hypotheses 2 and 3 concern the effect of seasonality. Where diversity is high, various species may provide foods in various seasons, thus may shorten the lean period (Janson & Chapman, 1999). These hypotheses have been tested individually (e.g. Balcomb et al., 2000), however, they are not mutually exclusive. To understand the relative importance of these hypotheses, we construct a linear model between density and these habitat variables.

Methods

ESTIMATING DENSITY OF MACAQUES

We censused a 29 km^2 area in the western area of Yakushima, where logging and hunting has been rare (Fig. 4-1). The altitude ranged from the coast to 1886m a.s.l. Censuses were conducted in July and August 1993, 1994, 1995, 1997 and 2000. Although censuses were conducted in a limited season, this does not bias the results considerably. Yoshihiro (1995) reported the highest limit of the distribution of Japanese macaques in Yakushima was 1886m a.s.l. in summer, but it descended to 1450m in winter. However, at about 1100m a.s.l., the centre of a troop's home range in summer was only 100m higher in elevation than that in the other seasons (Hanya, unpublished data). Large-scale seasonal migration has not been reported for coastal groups. Thus, although density around the summit may change in other seasons, density is expected seasonally stable in the other zones by using zonation more than 100 m.

We used point census described in detail in chapter 3. We divided each year's census period into one, two or four census terms, which lasted four days at most (Table 4-1). During each term, we censused areas of 2-7 km^2 Census area overlapped among different years. Census area was divided into 116 quadrates of 500

m × 500 m. In each quadrate, one observer was positioned at an observation point on a ridge. Observers simultaneously searched macaque groups visually and auditorially from 6:00-7:00 to around 15:00-16:00 as long as rain and wind was not strong. Besides, researchers followed groups which appeared in the census area whenever possible. Those researchers were not distributed in a systematic way, so their data was not used to estimate density, and used only to estimate group size.

Although 27 points were censused in different years, these data were pooled for analysis. Number of days censused for a point ranged from one to nine. Data of the points censused for only one day were discarded because the confidence limit of the number of groups detected becomes stabilized when censusing the points for more than a day (chapter 3). When the point was censused for less than six hours, the point's data on the day was discarded because detectability changes with the time of a day (chapter 3). The number of points used in the analysis was 101 in total.

The number of groups detected each hour by each point observer was averaged for that day, and averaged again for the entire census days. This value, number of groups detected per hour per point, was used as relative group density (RGD) in the following analysis.

We compared the RGD with the altitude of the points, classifying the altitude per 200 m in elevation (0-199 m, 200-399 m, etc). The highest zone (1600 m-) included points more than 1800 m a.s.l. After the analysis of RGD, we re-classified the vegetation post hoc based on the results of RGD and zonation by Kimura & Yoda (1984) to examine the altitudinal difference in habitat.

We have shown that RGD can be transformed into absolute group or population density (chapter 3). However, we did not estimate absolute density in this chapter because necessary parameters are not available in most of the zones. The validity using RGD as a representative of population density will be investigated in the discussion.

HABITAT

We compared four parameters of habitat characteristics; total basal area (TBA) of food trees, number of food species per unit area, seasonal fruit abundance, and total annual fruit production. All the data were from the western area. We determined food species by the data in chapter 5, Maruhashi (1980), and GH's unpublished data based on 500 hours of direct observation. These dietary data were from the western area, covering from the coast to 1200 m a.s.l.

Basal area of food trees. TBA (m^2/ha) of macaques' food species was compared among 24 plots. The sources are from authors' data and literature (Tagawa, 1980; Kohyama et al., 1984; Kimura & Yoda, 1984; Okada & Ohsawa, 1984; Tagawa et al., 1984). The area of the plots ranged from 0.04 ha to 2.48 ha. The altitude ranged from 120 m to 1590 m a.s.l. Although the minimum DBH measured differed among plots (0-5 cm), this did not affect the results considerably because the basal area of smaller trees are negligible compared to larger trees. In plots where DBH of all the trees were measured, the basal area of trees with a DBH=0~5 cm occupied only 5.9% (600 m a.s.l.), 2.5% (1050 m), or 1.6% (1060 m) of the TBA.

Number of food species. Number of food species per unit area was compared along a road which ran from 30 m to1100 m a.s.l. The road was divided into 188 segments, each of which was 100 m long. For each segment, we recorded the species that were visible within 5 m from the road. Shrubs shorter than 1 m were not recorded.

Seasonal fruit abundance. Altitudinal difference in seasonal fruit abundance was assessed by monthly or bimonthly changes of wet weight of fleshy parts per hector. Three plots were set; the altitude was 280 m, 600 m, 1050 m, and the area covers 0.225 ha, 0.25 ha, and 0.5 ha, respectively. At the 280 m plot, species and DBH of trees taller than 0.5 m were recorded. At the 600 m and 1050 m plots, species and DBH of

trees >5 cm DBH was recorded. To sample smaller trees within the 600 m and 1050 m plots, we randomly set 10 (600 m) or 20 (1050 m) 5 m × 10 m subplots, and recorded DBH and species of trees taller than 1 m. The study terms of seasonal fruit abundance were: 280 m, October 1988 to November 1989; 600 m, October 1999 to March 2001; 1050 m, May 1999 to March 2001.

Protocol to estimate the fruit abundance differed between the 280 m plot and the others. At the 600 m and 1050 m plot, the number of ripe and unripe fruits of a marked branch was counted at the onset of the study. The total crop of the individual tree was estimated by the percentage in volume of the branch to the total crown. Later, we checked only presence/absence of ripe fruits of all trees twice a month. When we found a new tree individual bearing unripe fruits, the number of fruits of the tree was counted. To estimate the number of ripe fruits when the tree was observed to have them, two assumptions were made. First, the number of fruits started decreasing when the tree was first observed to be ripe (i.e. more than half of the fruits in that tree are ripe). Second, fruits decreased linearly until they were completely consumed. These assumptions are sometimes true but not always (Noma & Yumoto, 1997). However, this procedure is expected, at least, to give a more precise estimate of fruit abundance than using the number of fruiting trees. According to these assumptions, suppose fruits disappeared at the *n*th census since the tree was first observed to be ripe, the number of fruits at the *k*th census is calculated to be: (estimated number of fruits in the tree before ripening) × {1-(k-1)/(n-1)}. Number of fruits at each fruiting census was weighed by the unit wet weight of the fleshy parts for the species. For short trees (<5 cm in DBH), wet weight of the fleshy parts was weighed by 10 because short trees were sampled for only one-tenth of the plots. Wet weights of all the trees were summed to calculate the fruit abundance at each time of the fruiting census.

At the 280 m plot, number of ripe fruits in marked branches was counted directly every time of fruiting census, conducted once or twice in a month (Noma &

Yumoto, 1997). Other protocol was the same as at the 600 m and 1050 m plots.

The number of species which fruited during the fruiting census was 29, six and 10 at the 280m, 600m and 1050m plots, respectively. All of these fruits were included in the macaques' diet. The number of trees which fruited during the fruiting census was 128 (569 trees/ha), 96 (384 trees/ha) and 208 (416 trees/ha) at the 280m, 600m and 1050m plots, respectively.

Total annual fruit production. We estimated the total annual fruit production at the same three plots as the seasonal fruiting census. Due to the limited fruiting seasons in this area, Noma, (1997) showed that it is possible to estimate the total annual production by counting fruits twice or once each year because abortions of fruits are already over and the consumption by frugivores has not begun by those times of year. The seasons are May and mid October to early November at the 280 m, October at the 600 m and late August or early September at the 1050 m plot. Total annual production in 1999, 2000 and 2001 was estimated by counting ripe and unripe fruits during those times of year. Data on the number of fruits were translated to the total wet weight of fleshy parts per hector.

Results

DENSITY OF MACAQUES

Relative group density (RGD, groups/hour/point) was significantly higher in 0-199 m and 200-399 m zones, and there were little differences between the other zones (Fig. 4-2). RGD also tended to be high in the highest zone (1600m-), however, the data were too few to conclude.

Based on this result, we re-classified the vegetation into four zones; coastal forest (0-399 m), broad-leaved forest (400-799 m), lower coniferous forest (800-1199 m), and higher coniferous forest (1200-1699 m). The summit area (1700 m-) will not be considered hereafter because no data on this habitat were available.

Our data on group size is preliminary because few groups were counted in the higher zones. There was no significant difference in group size between zones (Table 2, Kruscal-Wallis test, $H=3.5$, $p>0.1$).

HABITAT

The correspondence between altitudinal variations of total basal area (TBA) of food trees and that of the RGD was larger for high-quality foods (fruits, seeds) than for low-quality foods (leaves, flowers, other foods). TBA of trees which provide high-quality foods decreased with altitude, while TBA of low-quality foods increased or did not change with altitude (Fig. 4-3). However, the correspondence between RGD and TBA of high-quality foods was not exact: the largest decrease of TBA was between broad-leaved and lower coniferous forests, in contrast to RGD, of which the largest difference was between coastal and broad-leaved forests.

Number of food species per unit area also decreased with altitude for most the food categories, however, the agreement with the RGD was partial. Number of species continuously decreased significantly with altitude for most of the food categories (Fig. 4-4), in contrast to the discrete changes of RGD.

Comparisons of seasonal fruit abundance (Fig. 4-5) indicated that the lean period when no fruit was available was longer in higher zones. This altitudinal change was continuous, and differed from the discrete changes of the RGD. The periods when no fruit was found in the plots were 5.9%, 22% and 50% of the total fruiting census period in the coastal, broad-leaved and lower coniferous forests, respectively.

Altitudinal variation of total annual fleshy fruit production was in accordance with that of the RGD. The fruit production was the largest in the coastal forest, and did not differ between the broad-leaved and lower coniferous forests (Table 4-3). Although inter-annual variations within the plots were four-fold at most, the production in the coastal forest was consistently the highest in all the three years.

To examine the explanatory powers of the habitat variables on mean RGD (X), we conducted multivariate analysis. Four variables were examined: TBA of fruit and seed foods (A), number of fruit and seed species per unit area (B), rate of lean period when no fruits were available to the entire fruiting census period (C), and total annual fleshy fruit production (D). Low-quality foods were excluded from the model a priori because of their apparent discrepancies with the RGD. Data in the higher coniferous forest was not used. After normalizing the explanatory variables, principal component analysis was conducted. The first and second principal components were calculated as $z_1=0.49A+0.53B-0.53C+0.44D$ and $z_2=0.59A+0.06B-0.06C-0.80D$. The first principal component evaluates the four variables equally, and the second component expresses the abundance of fruits independent of seasonality. According to multiple regression analysis, the partial regression coefficients were calculated as 0.065 for z_1 and 0.193 for z_2. Thus, abundance of fruits independent of seasonality has a stronger explanatory power.

Discussion

POTENTIAL BIAS

Because we did not estimate absolute density, we discuss the potential bias in our results, then consider the effect of habitat variables.

First, the difference in group size among zones may affect the relative population density. Group size was not counted in the broad-leaved forest, however, Yoshihiro et al. (1999) reported that the group size in this zone (23, n=5) did not differ significantly from the coastal or the lower-coniferous forests. Even when we suppose that group size is different among zones (but could not be detected statistically), the relative population density in the coastal forest will still be the largest because the observed group size was the largest in this zone. The RGD in the coastal forest may be an underestimate as relative population density.

Second, detectability may differ with altitude. In chapter 3, it was shown that the detectability was not biased with topography or habituation of groups. The difference in group size among zones, if any, may have overestimated the RGD in the coastal forest because of the larger group size thus higher detectability in this zone. However, this overestimate is unlikely to affect our findings for two reasons. First, this overestimate is canceled out exactly by an underestimate of relative population density (see above), supposing detectability is proportional to the mean group size (Buckland et al., 1993). Second, the observed variation in group size was too small to account for the two- or three-fold difference in the RGD.

DETERMINANTS OF DENSITY

We have shown that the relative group density (RGD) of Japanese macaques in Yakushima is high in the coastal forest, and did not differ between the higher zones. Comparisons of habitat variables indicated that all the four hypotheses were supported at least partially. (1) Variation in RGD corresponded to the availability of high quality foods, not the low-quality foods. RGD was high where (2) diversity of food species was high, (3) the length of lean period was short, and (4) total annual production of fleshy fruits was high. Among the habitat characteristics, altitudinal variation of RGD was most identical with that of the total annual fleshy fruit production.

We have shown the importance of the quantity of high-quality foods rather than low-quality foods as a determinant of RGD. It is also reported that the amount of high-quality foods correlated to the density of chimpanzees (Balcomb et al., 2000), or granivorous and/or frugivorous rodents (Wolff, 1996; Adler, 1998; Choquenot & Ruscoe, 2000). On the other hand, densities of colobines and folivorous lemurs are reported to be limited by the quality of mature leaves (Waterman & Ross, 1988; Oates et al., 1990; Ganzhorn, 1992). These examples may suggest the different mechanisms of resource limitation between folivores and generalists/frugivores. Folivores may be

regulated by the quality of leaves because leaves are super-abundant but entail digestive problems. Generalists and frugivores are unable to digest leaves effectively. They may be limited by the quantity of fruits or seeds because those high-quality foods are usually limited in quantity (Janson & Chapman, 1999). However, this proposition cannot be generalized until both quality and quantity of high- and low-quality foods are quantified.

Food species diversity, or more directly, lean seasons in the availability of high-quality foods are often assumed to determine animal densities (e.g. Milton, 1982; Chapman & Balcomb, 1998). Number of food species or length of lean period may have worked in regulating the density of Japanese macaques in Yakushima, however, explanatory powers were weak compared to total annual fleshy fruit production. Japanese macaques survive the lean period when few fruits are available not only by the food available at that time, but also by consuming fat deposited during the period of high fruit availability. Larger fruit production sustains more individuals to deposit fat to survive the lean period. Fat deposition also enhance the reproductions of female Japanese macaques (Mori, 1979). Therefore, the altitudinal variation of total annual fruit production correlates to that of density.

It should be noted the above discussion is about the comparisons within Yakushima. The main food during the lean period is mature leaves in all the zones (Agetsuma, 1995; Hanya, Noma & Agetsuma, unpublished data). Mature leaves satisfies about 90% of the daily energy requirement (Iwamoto, 1982), thus, compared to other populations, the lean period may not be so severe as to regulate densities.

The importance of lean period is suggested by species-wide comparisons of population densities of Japanese macaques (Table 4). Population densities in evergreen forests, including Yakushima, are consistently higher than those in deciduous forests. Main foods during the lean period are mature leaves in evergreen forests, buds or barks in deciduous forests. In deciduous forests, Japanese macaques' daily energy

intake is only 56% of the requirement (Nakagawa, 1989). Japanese macaques in deciduous forests are required to deposit more fat, thus need larger per-capita home range area than in evergreen forests supposing the production of high-quality food is constant. In fact, decrease in body weight by wintering Japanese macaque is large in deciduous forest (10%; Wada, 1975) than in evergreen forest (5%; Mori, 1979). Therefore, the amount of high-quality foods and severity of lean periods both regulate the density of Japanese macaques in terms of fat deposition.

An adaptation to 'store' high-quality foods, such as fat deposition, is important to understand the effect of seasonality on resource limitation. The importance of this adaptation may be reinforced by population regulation of frugivorous rodents on Barro Colorado Island, Panama (Smythe, Glanz & Leigh, 1982). During lean periods, pacas relied on leaves, while agoutis ate scatter-hoarded seeds. The effect of poor fruiting on density was more severe for agoutis. Scatter-hoarding may be analogous to fat deposition in that both are adaptations to store high-quality foods during the lean periods. Densities of agoutis was affected by the amount of high-quality foods because they relied on fruits even during the lean periods in terms of scatter-hoarding, as well as the densities of fat-depositing Japanese macaques in Yakushima was.

In conclusion, the combination of annual total fruit production and the food condition during the lean period determines the density of Japanese macaques. Larger fruit production sustains more macaques to deposit fat to survive the lean period, and the better food conditions during the lean period, such as mature leaves in Yakushima, require macaques fewer fat to be deposited, thus enable larger densities.

Chapter 5: VARIATIONS IN DIET

Introduction

Primate diet is generally predictable by body weight and digestive features linked to phylogeny (Clutton-Brock & Harvey, 1977; Gaulin, 1979). However, their diet is variable even within the species (e.g. guenons, Gautier-Hion, 1983; chimpanzees, Nishida et al., 1983; Japanese macaques, Agetsuma & Nakagawa, 1998). Some primate species change their diet in response to their environmental changes (Hladik, 1981), but some do not (e.g. tamarins: Garber, 1993). Chapman & Chapman (1990) reviewed the diet of 46 primate populations, and found that dietary variability was not constrained by phylogeny, main diet categories (insects, fruits, etc.), body size, population density, sympatric primates, habitat productivity and seasonality. However, more rigorous comparison may be possible by using other measurements, such as coefficient of variation or overlap between monthly dietary composition. The adaptive significance of dietary variability would be clarified best by studies on primates in temperate regions, because primates there experience a harsh winter and a long lean period when no fruit is available (Thompson & Wilson, 1979; Herrera, 1984).

Japanese macaques live at the northern limit of nonhuman primate distribution. Their habitats vary from warm-temperate broad-leaved evergreen forest (including subtropical vegetation) to cool-temperate deciduous forest (covered with several meters of snow in winter) (Yamagiwa & Hill, 1998). Seasonal variations in these habitats are great in accordance with the changes in day length and temperature. Their seasonal and/or regional variations of diet are indispensable for understanding the breadth of adaptability primates have (Nakagawa et al., 1996; Agetsuma & Nakagawa, 1998). A systematic description of their diet for more than a year is found only in the lowland forest in Yakushima (Hill, 1997), the southern limit of their distribution.

Yakushima is an ideal site for studying the dietary variation of Japanese

macaques. Here, within-population variation in habitat is expected to be the largest for this species. In Yakushima, Japanese macaques are continuously distributed from coastal warm-temperate broad-leaved evergreen forest to subalpine summit (Yoshihiro et al., 1999). The lowland forest is the richest habitat for this species in terms of food productivity and climate (Maruhashi, 1980). On the other hand, the summit may be climatically similar to the northern limit of the species distribution (Eguchi, 1984). We conducted a two-year survey on their dietary variation with altitudinal differences. Our main objective is to understand the effect of environmental factors on seasonal, altitudinal and inter-annual dietary variations of Yakushima macaques. Furthermore, we examine the quantitative relations between seasonal variability in their diet and fruit abundance by altitudinal comparisons within their habitats. We discuss the adaptive significance of dietary variability in response to habitat variability.

Method

HABITAT

As in chapter 4, four habitat variables were compared: total basal area (TBA) of food trees, number of food species per unit area, seasonal fruit abundance, and total annual fruit production. The method is described in chapter 4 in detail. The differences with data in chapter 4 are: (1) habitat in the higher coniferous forest was not analysed, because dietary data was not available here and (2) food species defined here was confined to only those identified in the faecal analysis, thus all were seed/fruit species.

DIET

We studied the diet of Japanese macaques by faecal analysis. We collected faecal samples on and around a road in the western area of this island (Fig. 4-1). We collected the samples from April 1999 to March 2001, although no sample was

collected in August 1999 in the lower coniferous forest. The total number of samples was 934 (Table 5-1). The number of samples in each month in each zone ranged from 5 to 26 (mean: 13.2). The minimum and maximum altitudes of samples were 30m and 1230m a.s.l.

Faeces were washed through 1mm meshes, and dried in an incubator at about 60° C for 2-3 hours. Each sample was categorized into seed/fruit, fiber (including leafy particles), animal matter, fungi and others. Sand was abandoned because of possible contamination during collection. Seed/fruit were identified whenever possible. The remains of each category were weighed, and the ratio in dry weight was calculated for each category for each dried sample, and is referred to as relative dry weight (RDW) hereafter.

We assessed the seasonal and altitudinal variability of the macaques' diet by 'similarity index', defined as the sum of the shared percentage in RDW of each category (Chapman, 1987). A lower similarity indicates a higher variability.

Results

VEGETATION AND FRUIT AVAILABILITY

In the faecal analysis, 66 species were identified as seed/fruit foods of Yakushima macaques. Altitudinal comparisons of vegetation indicated that more seed/fruit foods were available in terms of TBA in the coastal and broad-leaved forest than in the lower coniferous forest (Turkey-Kramer test: coastal vs. lower coniferous, $t=-3.72$, $p<0.01$; broad-leaved vs. lower coniferous, $t=-3.99$, $p<0.01$; coastal vs. broad-leaved, $t=1.31$, $p>0.1$; Fig. 5-1a). The number of seed/fruit species per unit area was significantly higher in the lower zones (coastal vs. broad-leaved, $t=6.25$, $p<0.001$; broad-leaved vs. lower coniferous, $t=-12.2$, $p<0.0001$; coastal vs. lower coniferous, $t=-16.9$, $p<0.0001$; Fig. 5-1b)

Total annual fleshy fruit production was greater in the coastal forest (1999,

112 kg of fleshy parts/ha; 2000, 81 kg/ha) than in the broad-leaved and lower coniferous forests (broad-leaved; 1999, 35 kg/ha; 2000, 47 kg/ha: lower coniferous; 1999, 23 kg/ha; 2000, 21 kg/ha). Macaques ate all the fruit species which fruited in the plots.

Comparisons of fruiting phenology indicated that (1) fruits were available for a longer period in the lower zones (Fig. 4-5) and (2) variability in seasonal fruit abundance increased with altitude. Although all the zones experienced periods when no fruit was found in the plots, this lean period was shortest in the coastal forest (<1 month), intermediate in the broad-leaved forest (5 months) and longest in the lower coniferous forest (7-8 months). For the entire study period, the coefficient of variation (CV) in the lower coniferous forest (1.78) was higher than in the coastal and broad-leaved forests (1.20 and 1.17, respectively). However, this may result from the different study duration among plots. When recalculated for the first or last 12 months of the study period, the CV was lowest in the coastal forest (1.08 or 1.25), intermediate in the broad-leaved forest (1.38) and highest in the lower coniferous forest (1.64 or 2.15).

OVERALL DIETARY PATTERNS

Macaques in the lower zones ate more seed/fruit and animal matters, and in the higher zones, they ate more fiber and fungi in both years (Table 5-2). The other category consisted of flowers and bark, which was only 0.1% in RDW.

The macaques had a different diet in different seasons (Fig. 5-2), and variability increased with altitude. The mean$\pm$standard deviation of the similarity index between different months of the same zone was 70$\pm$20%, 64$\pm$21%, and 54$\pm$27% for the coastal, broad-leaved and lower coniferous forest, respectively. The differences among zones were significant (Wilcoxon's signed rank test: coastal vs. broad-leaved, $z=-4.27$, $n=276$, $p<0.0001$; broad-leaved vs. lower coniferous, $z=-5.04$, $n=253$, $p<0.0001$; lower coniferous vs. coastal, $z=-8.51$, $n=253$, $p<0.0001$).

An annual cyclicity of the dietary composition was found on a monthly basis. Similarity indices between same calendar months were significantly larger than other pairs in the lower coniferous forest ($n1=11$, $n2=242$, $U=1150$, $p<0.05$) and nearly significantly larger in the broad-leaved forest ($n1=12$, $n2=264$, $U=1078$, $p=0.06$), but did not differ in the coastal forest. However, the cyclicity may have been diluted by similarity between successive months. In fact, when successive month-pairs are excluded, the difference was nearly significant in the coastal forest ($n1=12$, $n2=231$, $U=1020$, $p=0.08$).

Although the macaques' diet tended to be annually cyclic, there were also inter-annual variations (Fig. 5-2). Similarity indices between the same calendar-month pairs ranged 57-91%, 40-98% and 41-98% in the coastal, broad-leaved and lower coniferous forests. In all the zones, inter-annual variation was small in autumn (September-November; Fig. 5-2).

The macaques' overall diet changed continuously with altitude. Similarity indices between adjacent (coastal/broad-leaved and broad-leaved/lower coniferous) zones in the same month ranged from 23 to 98%. Monthly similarity indices between the coastal/broad-leaved were not significantly different from those between the broad-leaved/lower coniferous (Wilcoxon's signed rank test: $n=23$, $z=-0.882$, $p>0.1$). On the other hand, similarity indices between the coastal/lower coniferous were significantly lower than adjacent zone-pairs (vs. coastal/broad-leaved, $n=23$, $z=-3.102$, $p<0.01$; vs. broad-leaved/lower coniferous, $n=23$, $z=-2.159$, $p<0.05$). These results mean that the dietary composition of macaques in the broad-leaved was similar to neither the coastal nor lower coniferous forests, but the intermediate.

VARIATIONS IN SEED/FRUIT-EATING

RDW and species composition of seed/fruit matters differed between zones (Fig. 5-2; Table 5-3). Seed/fruit was the most important food category in the coastal

and broad-leaved forests in RDW of the two years. In the lower coniferous forest, it was the second most important category, after fiber. Defining the main items as those of which the RDW during the two years were at least 1% in each zone, the number of seed/fruit main items was 17, 19 and 10 in the coastal, broad-leaved and lower coniferous forest, respectively (Table 5-3).

Although macaques ate the most seed/fruit in autumn (September-November) and the least in spring (March-April) in all the zones, seasonal patterns were different between zones. Macaques depended on seed/fruit for a longer time of year in the lower zones. In the lower coniferous forest, almost no seed/fruit was found in faeces from February to May.

The monthly changes in RDW of seed/fruit was significantly correlated to the average fruit abundance of the months in the lower coniferous forest, but did not correlate significantly in the broad-leaved forest (Spearman's rank correlation: broad-leaved forest, $r=-0.213$, $p>0.1$; lower coniferous forest, $r=0.708$, $p<0.01$). This result suggests that in the broad-leaved forest, macaques utilized fruits selectively and depended on rare species.

Considering that seasonal changes in the overall seed/fruit abundance in the forest was not enough to explain the altitudinal differences in seasonal patterns of frugivory, we examined the consumption patterns of each main item in each zone (Table 5-3). We classified the main foods into four types by the seasonal pattern of appearance. These types, though not discrete but rather continuous, would be useful to understand the differences between zones. *Figs* were used for a prolonged period (5-11 months/year). *Early summer types* were eaten heavily around May or June. *Summer/Autumn types* include many species which started being eaten in August to December. *Spring type* was used in April-May.

The lower coniferous forest lacked figs and spring type (Table 5-3). Consequently, there was a long period when macaques ate no fruits in the winter and

spring. In the coastal and broad-leaved forests, all of the four types existed (Table 5-3). In particular, macaques in the coastal forest consumed *Ficus superba* in a large amount from April until November. The existence of figs and spring type foods must have contributed to the long period when macaques relied on seed/fruit heavily in the lower zones.

VARIATIONS IN FIBER, ANIMAL MATTER AND FUNGI-EATING

Macaques ate fibrous foods and fungi when and where seed/fruit foods were not available. Animal matters were eaten irrespective to the availability of seed/fruit foods.

Fiber was the most important category for the macaques in the lower coniferous forest, while it was the second most important food in the coastal and broad-leaved forest. There was a negative correlation between RDW of fiber and seed/fruit in all the zones (Spearman's rank correlation, coastal: $r=-0.904$, $p<0.0001$; broad-leaved: $r=-0.943$, $p<0.0001$; lower coniferous: $r=-0.956$, $p<0.0001$). RDW of fiber had its peaks in spring (March-April), and low points in autumn (September-November; Fig. 5-2). The foliage-dominated period was more prolonged in the higher zones.

Animal matter had a relatively small RDW. It was especially high in the coastal forest. It increased in the summer (July-August), and decreased to almost nothing in winter (Fig. 5-2). However, in the coastal forest, animal matter was high even from May to November. Although most of the particles were too fragmented to be identified, they were mostly chitin particles of insect exoskeletons.

Macaques in higher zones ate more fungi than in lower zones. In the coastal and broad-leaved forests, the seasonal change in RDW of fungi was negatively correlated with that of seed/fruit (coastal, $r=-0.480$, $p<0.05$; broad-leaved, $r=-0.486$, $p<0.05$; Fig. 5-2).

Discussion

RELIABILITY OF FAECAL ANALYSIS AS A METHOD OF STUDYING DIET

Faecal analysis has been rarely used to study medium-sized primates like Japanese macaques (but see Su & Lee, 2001). According to Atsalis (1999), the disadvantages of faecal analysis are as follows: (1) Overrepresentation of seed/fruit items and underrepresentation of soft food items such as gum, flowers, buds and soft-bodied invertebrates. (2) Underrepresentation of seeds which are not swallowed. (3) Impossibility of identification of leaf foods. Faecal analysis, however, is a useful method when studying seasonal and/or regional variations in dietary composition (Atsalis, 1999). Regional or seasonal variation is an essential aspect of primate diet, considering its flexibility (Hladik, 1981). In particular, faecal analysis makes it possible to study the diet of non-habituated animals, which are difficult to observe.

We examined the bias in faecal analysis by comparing the present results in the coastal forest with previous studies by direct observation (Agetsuma, 1995; Hill, 1997; Otani & Shibata, 2000). The seasonal pattern in time spent on feeding leaves, seeds, fruits and insects are quite similar to that of relative dry weight (RDW). However, they reported peaks of fallen-seed eating, in particular acorns of *Lithocarpus edulis*, in January-February. This peak was not found by faecal analysis because of the inability of detecting acorns by faecal analysis. Among the 25 seed/fruit species listed by Otani & Shibata (2000), 6 species were not included in our list. Among them, 3 species were acorns and the others were not distributed or did not fruit in this study.

How did this bias misrepresent the seasonal and altitudinal pattern of diet? First, data were not biased in higher zones, because *L. edulis* are distributed up to 900m a.s.l. (Hanya, unpublished data). Second, seed/fruit consumption in winter was underestimated in lower zones, because our data does not include acorn-eating during this period in those zones. Therefore, the altitudinal difference in winter must have been larger than what was reported here.

ALTITUDINAL, SEASONAL AND INTER-ANNUAL VARIATION OF DIET

The purpose of the present study was to understand the determinants of altitudinal, seasonal and inter-annual variation of the diet of Yakushima macaques, and examine the relationship between habitat and dietary variability. Our results are summarized as follows: Concerning the habitat, (1) total basal area of seed/fruit food trees was smaller in the lower coniferous forest. (2) Number of seed/fruit species available per unit area was larger in the lower zones. (3) Fleshy fruit production was large in the lowest zone. (4) Variability in seasonal fleshy fruit production increased with altitude. (5) Fruits were available for longer periods in the lower zones. Concerning the diet, (6) in lower zones, macaques ate more seed/fruit and animal matter, and less fibrous foods and fungi. (7) Diet changed continuously with altitude. (8) Figs and spring-borne fruits were not available to macaques in the highest zone. (9) Dietary variability increased with altitude.

What causes the seasonal, altitudinal and inter-annual variations in the diet of Yakushima macaques? Most of their diet consists of seed/fruit and fibrous materials, and the seasonal changes in RDW of these two categories were complementary. In Yakushima, evergreen leaves are available in all zones, and macaques were observed to eat evergreen leaves (coastal forest: Agetsuma, 1995; Hill, 1997; lower coniferous forest: Hanya, unpublished data). Mature leaves are available in all seasons at any altitude, and it is known that mature leaves are eaten only when preferred foods are not available in the coastal forest of Yakushima (Agetsuma, 1995). Young leaves are consumed in response to the increased availability, but they are eaten for only a limited period, and the amount is much smaller than the amount of mature leaves (Agetsuma, 1995; Hill, 1997). Thus, it is reasonable to suppose patterns of seed/fruit consumption determines overall dietary composition. Then, what causes the variation of seed/fruit consumption?

Seed/fruit production and its species composition seemed to be the principal

factor determining the variation of seed/fruit consumption. In the coastal forest, fruit production or density of seed/fruit trees was highest, and species diversity was also highest. Some rare species, especially figs sustained the macaques in this zone for a long time. These explain the longest period when macaques relied on seed/fruit heavily in the coastal forest. In the lower coniferous forest, fruit production or density of seed/fruit trees was lowest, species diversity was lowest, and some types of seed/fruit food species (such as figs or spring-borne *Litsea acuminata*) were lacking. These explain the shortest period when macaques relied on seed/fruit heavily in the lower coniferous forest. In the broad-leaved forest, fruit production and seed/fruit species diversity was lower than the coastal forest, but density of the composition of the main items was similar to that of the coastal forest. These explain the intermediate period when macaques relied on seed/fruit heavily in the broad-leaved forest. Thus, continuous altitudinal dietary variation was caused by the altitudinal variation in seed/fruit availability.

There were also seasonal and altitudinal variations in consumption of animal matters and fungi. Macaques seemed to eat animal matters when and where temperature was high. Insects were probably more available when temperature was high (Agetsuma, 1995). Macaques might eat fungi when fruits are scarce, at least in the coastal and broad-leaved forest.

Yakushima macaques generally showed annually cyclic patterns of dietary shifts on a monthly basis. This is contrastive to three Costa Rican primates, which exhibit no cyclicity of diet (Chapman, 1987). This difference may suggest that seasonal change is more predictable in temperate forest than in tropical rain forest. However, more populations should be compared before making a conclusion on the difference in annual cyclicity of diet. The inter-annual variations were small in autumn. This was probably because many species fruited in autumn, so the effect of inter-annual differences in fruit production of each species (Noma, 1997) was canceled

out. In other seasons, number of available seed/fruit species was small, thus overall dietary composition would be influenced by only a few species, such as *Myrica rubra* in the early summer (Hill & Agetsuma, 1995). Thus, it was suggested that inter-annual variation or cyclicity of the diet was also caused by the variation of seed/fruit availability.

ADAPTIVE SIGNIFICANCE OF DIETARY VARIABILITY

Contrary to Chapman & Chapman (1990), altitudinal comparisons of Yakushima macaques indicated that the seasonal dietary variability was high where seasonal variability in fruit abundance was high. The Yakushima macaque example suggests that dietary variability is a response to seasonally variable environments in terms of the availability of high quality foods.

This conclusion cannot be generalized very much because few studies have quantified variability of diet and habitat as has the present one (but see Chapman, 1987). However, qualitative comparison is possible, in particular in the long period (5 months in a year) when Yakushima macaques ate no fruits in the lower coniferous forest, which was the main cause of high dietary variability in this zone. This is quite a long period for large- or medium-sized non-forestomach fermenter anthropoids (e.g. *Macaca fascicularis*, Yearger, 1996; *M. nigra*, O'Brien & Kinnaird, 1997; *M. radiata*, Ali, 1986; *M. nemestrina*, Caldecott, 1986; *Lophocebus albigena*, Poulsen et al., 2001; *Mandrillus sphinx*, Hoshino, 1985; *Cercopithecus* spp., Gautier-Hion, 1980; *Pongo pygmaeus*, Galdikas, 1988; *Pan troglodytes*, Yamakoshi, 1998; *Hylobates agilis*, Gittins, 1982; *Callicebus torquatus*, Palacios et al., 1997; *Cebus apella*, Galetti & Pedroni, 1994; *Alouatta pigra*, Silver et al., 1998; *Lagothrix lagotricha*, Peres, 1994; *Brachyteles arachnoides*, Strier, 1991). These species usually do not experience season when they do not eat seed/fruit at all. Exceptions are macaques in temperate regions (*M. cyclopis*: Su & Lee, 2001; *M. sylvanus*: Mehlman: 1988; *M. mulatta*: Goldstein &

Richard, 1989), baboons (*Papio cynocephalus*: Post, 1982), patas monkeys (*Erythrocebus patas*: Isbell, 1998), and mountain gorillas (*Gorilla gorilla beringei*: Watts, 1984). The habitats of these species, including Japanese macaques, are marginal for primates. In addition, they are often the only primate species there. In these marginal habitats, fruit production is highly seasonal (temperate forest, this study) or very sporadic (high mountains of mountain gorillas' habitat, Watts, 1984). The ability to include low-quality foods, at least for a part of the year, is necessary in these habitats. These facts suggest dietary variability, probably in response to a seasonally variable environment, was an essential adaptation to make their radiation into marginal habitats possible.

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Table 3-1. Comparison of detectability constant

a. troop*

OM	PE	SY
(37/480)	(23/268)	(47/519)
29.5	29.3	27.8

b. time of day

6:00-9:00	9:00-12:00	12:00-
(34/362)	(44/512)	(39/518)
12.6	32.5	30.4

c. distance from nearest ridges

-200m	200m-300m	300m-
(7/264, 4 points)	(46/418, 11 points)	(64/710, 13 points)
33.1	31.4	27.9

d. distance from rivers

-200m	200m-
(30/425, 8 points)	(87/867, 20 points)
30.5	26.7

e. difference between minimum and maximum altitude in quadrate

-200m	200m-
(60/732, 11 points)	(57/660, 17 points)
30.8	30.2

f. day

first two days	second two days	last two days
(31/350)	(39/559)	(47/483)
34.2	26.3	23.5

Values in the parentheses indicate #distance data/#detection at points, and #points.
*HR troop was excluded because of the scarcity of data.

a. F-test: OM vs PE, $Fs=0.00012$, $p>0.1$; PE vs SY, $Fs=0.20$, $p>0.1$; SY vs OM, $Fs=0.16$, $p>0.1$.

b. F-test: 6:00- vs 9:00-, $Fs=5.09$, $0.05<p<0.1$; 9:00- vs 12:00-, $Fs=0.026$, $p>0.1$; 12:00- vs 6:00-, $Fs=12.5$, $p<0.01$.

c. F-test: -200m vs 200m-300m, $Fs=0.064$, $p>0.1$; 200-300m vs 300m-, $Fs=0.12$, $p>0.1$; 300m- vs -200m, $Fs=0.76$, $p>0.1$.

d. F-test: $Fs=0.95$, $p>0.1$.

e. F-test: $Fs=0.015$, $p>0.1$.

f. F-test: fisrt vs second, $Fs=1.46$, $p>0.1$; second vs last, $Fs=0.62$, $p>0.1$; last vs first, $Fs=3.62$, $p>0.1$

Table 4-1. Number of days and points in each census terms

Year	Date	Census term			Altitude (m)
		I	II	III	
1993	Jul20-Aug10	3	3		10~310
		9	8		
1994	Jul18-Aug06	4	2	4	30~1332
		9	8	21	
1995	Jul24-Aug12	4	4		900~1332
		17	15		
1997	Jul26-Aug07	4	2		920~1886
		23	25		
2000	Jul25-Aug09	6			620~1331
		28			

Upper: number of days census was conducted in each census term.
Lower: number of points sampled in each census term.

Table 4-2. Relative group density (RGD) and group size

Zone	Altitude (m)	RGD	Group size				
			N	Mean	SD	Max	Min
Coastal forest	0-399	0.41	27	21.7	9.7	46	7
Broad-leaved forest	400-799	0.13	0				
Lower cniferous forest	800-1199	0.20	5	15.8	5.1	24	10
Higher coniferous forest	1200-	0.21	3	13.6	1.5	15	12

Table 4-3. Altitudinal comparison of total annual fleshy fruit production

Zone	Altitude (m)	1999	2000	2001	Mean
Coastal forest	280	173	81	94	116
Broad-leaved forest	600	35	47	12	31
Lower coniferous forest	1050	23	21	41	28

Wet weight of fleshy parts (kg/ha) are shown.

Table 4-4. Population densities of Japanese macaques

Population	Habitat	Latitude (N)	Density (macaques/km^2)	Source
Yakushima, 0-300m	Evergreen	30	62-100	Yoshihiro et al., 1999 & this study
Koshima	Evergreen	31	71	Takasaki, 1981
Takasakiyama	Evergreen	33	67	Takasaki, 1981
Kawaradake	Evergreen	33	59	Takasaki, 1981
Yakushima, 900-1300m	Evergreen	30	36	Yoshihiro et al., 1999 & this study
Toimisaki	Evergreen	31	33	Takasaki, 1981
Yakushima, 300-900m	Evergreen	30	30-36	Yoshihiro et al., 1999 & this study
Kinkazan	Deciduous	38	18-27	Izawa, 1995
Shodoshima	Deciduous	34	12.7-13.8	Takasaki, 1981
Shimokita	Deciduous	41	8.2	Takasaki, 1981
Shiga Heights	Deciduous	36	4-5.6	Takasaki, 1981

Table 5-1. Number of faecal samples

Year	Month	Coastal forest	Broad-leaved forest	Lower coniferous forest	Total
1999	April	10	10	8	28
	May	18	12	7	37
	June	16	14	5	35
	July	14	14	10	38
	August	15	12		27
	September	15	13	21	49
	October	17	13	28	58
	November	10	14	18	42
	December	15	12	20	47
2000	January	14	12	10	36
	February	17	13	14	44
	March	15	13	15	43
	April	11	17	15	43
	May	14	10	13	37
	June	10	9	11	30
	July	14	9	10	33
	August	13	7	13	33
	September	12	9	24	45
	October	10	11	21	42
	November	13	10	21	44
	December	11	8	14	33
2001	January	13	9	15	37
	February	15	16	11	42
	March	11	12	8	31
Total		323	279	332	934

Table 5-2. Overall dietary patterns during the two years

	Seed/fruit	Fiber	Animal matter	Fungi	Other
Coastal forest	0.705	0.227	0.039	0.026	0.004
Broad-leaved forest	0.579	0.312	0.015	0.094	0
Lower coniferous forest	0.403	0.478	0.009	0.109	0

Mean relative dry weight of each category in each month was averaged for two years in each zone.

Table 5-3. Consumption patterns of main items

(a) Coastal forest

Type	Species	Family	RDW	Rank	1999 A	M	J	J	A	S	O	N	D	2000 J	F	M	A	M	J	J	A	S	O	N	D	2001 J	F	M
Fig	*Ficus superba*	Moraceae	7.9	1	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*		*
Fig	*Ficus erecta*	Moraceae	3.8	6				*	*	*	*	*	*	*					*	*	*	*	*	*	*	*		*
Fig	*Ficus pumila*	Moraceae	3.3	9				*	*	*	*	*	*								*	*	*	*	*			
Early summer	*Rubus* spp.	Rosaceae	3.5	7	*	*	*	*									*	*	*	*								
Early summer	*Myrica rubra*	Myricaceae	6.1	3		*	*											*	*	*								
Early summer	*Persea thunbergii*	Lauraceae	2.0	14		*												*	*	*								
Summer/autumn	*Mallotus japonicus*	Euphorbiaceae	1.1	16				*	*												*	*						
Summer/autumn	*Cornus macrophylla*	Cornaceae	1.1	17				*	*	*											*	*	*	*	*	*		
Summer/autumn	*Euscaphis japonica*	Staphyleaceae	2.7	11					*	*	*	*	*	*	*	*		*			*	*	*	*	*	*		
Summer/autumn	*Rhus succedanea*	Anacardiaceae	7.7	2					*	*	*	*	*	*	*	*					*	*	*	*	*	*	*	*
Summer/autumn	*Eurya* spp.	Theaceae	4.2	5					*	*	*	*	*	*	*	*					*	*	*	*	*	*		
Summer/autumn	*Neolitsea* spp.	Lauraceae	2.8	10						*	*	*	*	*									*	*	*	*	*	
Summer/autumn	*Distylium racemosum*	Hamamelidaceae	1.2	15						*	*										*							
Summer/autumn	*Fagara alianthoides*	Rutaceae	3.4	8								*	*	*	*						*			*	*	*		
Summer/autumn	*Morinda umbellata*	Rubiaceae	4.5	4									*	*	*	*									*	*	*	*
Summer/autumn	*Lysimachia sikokiana*	Primulaceae	2.6	12									*	*	*	*	*	*								*	*	*
Spring	*Litsea acuminata*	Lauraceae	2.3	13													*	*	*								*	*

(b) Broad-leaved forest

Type	Species	Family	RDW	Rank	1999 A	M	J	J	A	S	O	N	D	2000 J	F	M	A	M	J	J	A	S	O	N	D	2001 J	F	M
Fig	*Ficus pumila*	Moraceae	7.0	1				*	*	*	*	*	*	*	*						*	*	*	*	*			
Fig	*Ficus* spp.	Moraceae	2.5	9				*	*					*						*	*	*		*				
Fig	*Ficus superba*	Moraceae	1.6	13	*	*	*		*	*	*	*	*			*		*		*				*				*
Early summer	*Rubus* spp.	Rosaceae	3.4	6	*	*	*	*	*								*	*	*	*	*							
Early summer	*Prunus jamasakura*	Rosaceae	1.2	19		*												*	*									
Early summer	*Myrica rubra*	Myricaceae	5.9	2			*	*										*	*									
Summer/autumn	*Mallotus japonicus*	Euphorbiaceae	1.9	12					*	*												*						
Summer/autumn	*Vitis ficifolia*	Vitidaceae	1.3	16						*	*	*	*								*	*	*					
Summer/autumn	*Symplocos tanakae*	Symplocaceae	1.9	11						*	*	*	*	*	*	*	*					*						
Summer/autumn	*Neolitsea* spp.	Lauraceae	2.2	10						*	*	*	*	*									*	*				
Summer/autumn	*Eurya* spp.	Theaceae	2.9	7						*	*	*	*	*	*								*	*	*			
Summer/autumn	*Fagara alianthoides*	Rutaceae	1.5	15						*	*	*	*	*								*		*	*			
Summer/autumn	*Elaeocarpus japonicus*	Elaeocarpaceae	3.4	5							*		*	*		*						*	*	*	*		*	
Summer/autumn	*Distylium racemosum*	Hamamelidaceae	2.6	8							*										*	*	*	*	*			
Summer/autumn	*Symplocos prunifolia*	Symplocaceae	1.3	17							*	*	*	*	*													
Summer/autumn	*Myrsine seguinii*	Myrsinaceae	4.6	4									*	*	*									*	*	*	*	*
Summer/autumn	*Morinda umbellata*	Rubiaceae	1.6	14									*	*	*									*	*			
Summer/autumn	*Lysimachia sikokiana*	Primulaceae	1.2	18										*	*	*	*	*									*	
Spring	*Litsea acuminata*	Lauraceae	4.9	3										*			*	*	*								*	*

(c) Lower coniferous forest

Type	Species	Family	RDW	Rank	1999 A	M	J	J	S	O	N	D	2000 J	F	M	A	M	J	J	A	S	O	N	D	2001 J	F	M
Early summer	*Prunus jamasakura*	Rosaceae	3.3	4		*	*										*	*	*								
Early summer	*Rubus* spp.	Rosaceae	3.2	5				*	*										*	*							
Summer/autumn	*Symplocos myrtacea*	Symplocaceae	3.9	2					*	*	*										*	*	*				
Summer/autumn	*Cornus kousa*	Cornaceae	3.4	3					*	*											*	*	*				
Summer/autumn	*Distylium racemosum*	Hamamelidaceae	1.6	7					*	*	*	*									*	*	*	*	*		
Summer/autumn	*Eurya* spp.	Theaceae	12.8	1					*	*	*	*	*	*							*	*	*	*	*		
Summer/autumn	*Dendropanax trifidus*	Araliaceae	2.5	6					*	*	*	*	*	*	*							*	*	*	*	*	
Summer/autumn	*Symplocos tanakae*	Symplocaceae	1.3	8					*	*	*	*	*	*	*												
Summer/autumn	*Boehmeria holosericea*	Urticaceae	1.2	9							*	*												*	*		
Summer/autumn	*Ilex crenata*	Aquifoliaceae	1.2	10									*	*	*							*		*	*	*	

RDW refers to the average of mean relative dry weight of 23/24 months.

* indicates the item was found in the faeces in the month in the zone.

Underlined species fruited in the corresponding phenology plots.

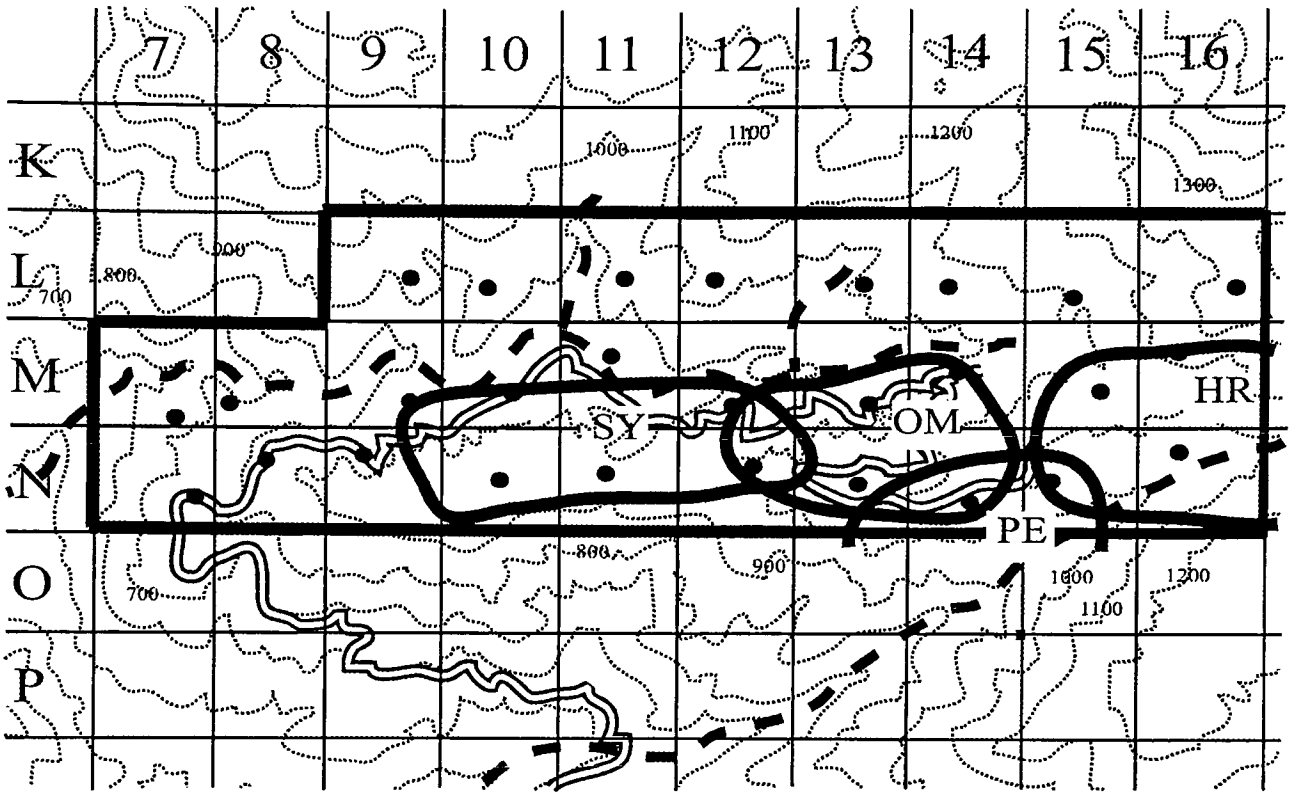

Fig. 3-1. Census area and home range of the four troops that were followed successfully. Filled circles indicate observation points. Double line indicates a road along which vegetation is disturbed. Dashed lines indicate rivers of widths more than 5 m. Contours are drawn per 100 m in altitude.

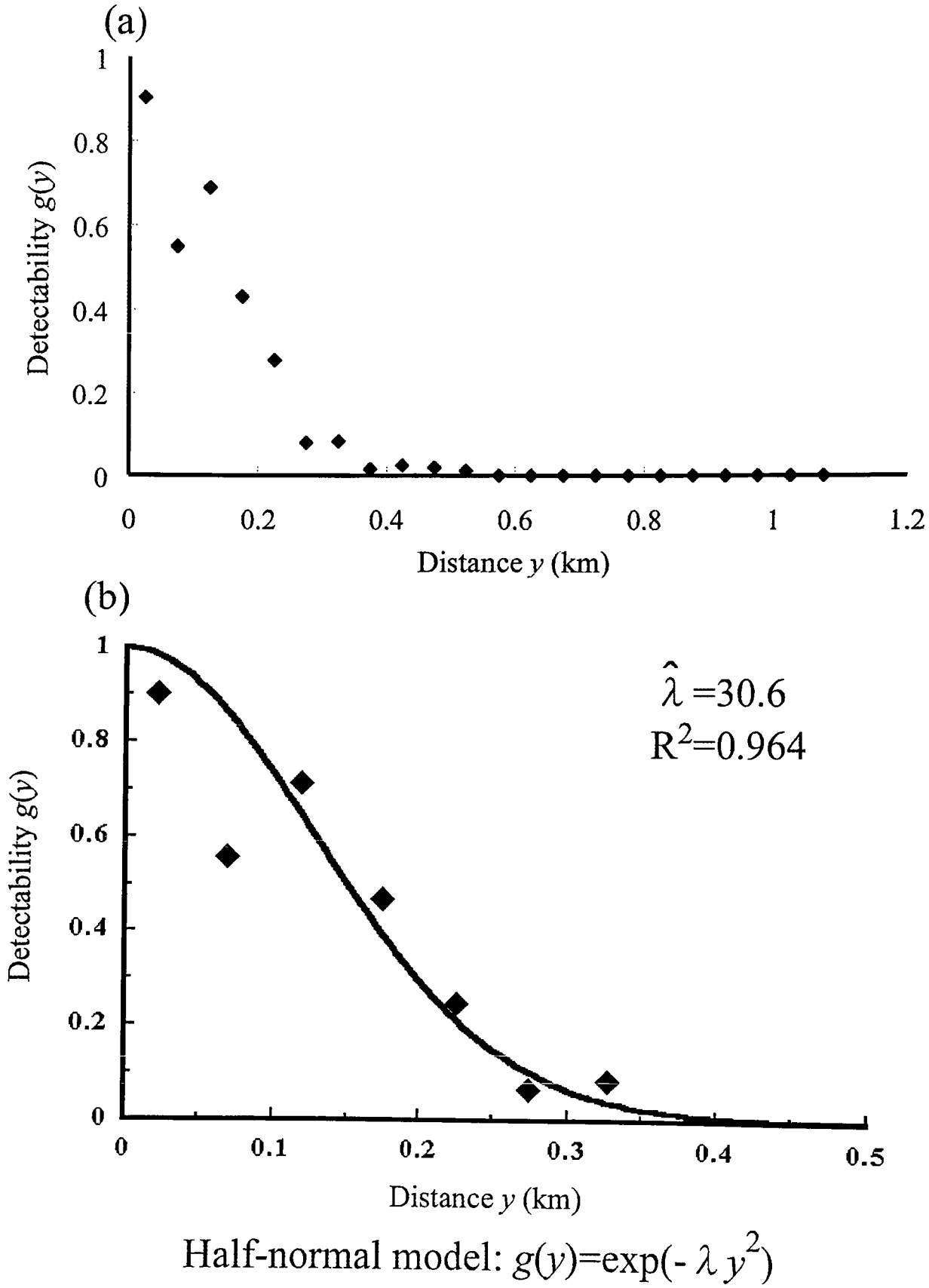

Fig. 3-2. Detectability of groups and distance from observation points. (a) Original data. (b) Detectability regressed on the half-normal model, after truncating the data of more than 0.35 km.

	7	8	9	10	11	12	13	14	15	16
L			0.29	0.16	0.03	0.10	0.21	0.15	0.10	0.10
M	0.09	0.00	0.64	0.06	0.05	0.17	0.23	0.06	0.10	0.02
N	0.16	0.13	0.00	0.32	0.17	0.19	0.30	0.19	0.38	0.06

(a) Number of groups detected

	7	8	9	10	11	12	13	14	15	16
L			3.04	1.61	0.25	1.00	2.16	1.48	0.95	1.00
M	0.93	0.00	0.39	0.59	0.51	1.75	2.37	0.55	1.00	0.16
N	1.59	1.35	0.00	3.39	1.73	1.94	3.18	1.94	4.14	0.64

(b) Estimated group density

Fig. 3-3. (a) Number of groups detected, averaged for the entire census period (four-six days). (b) Estimated group density for each observation point.

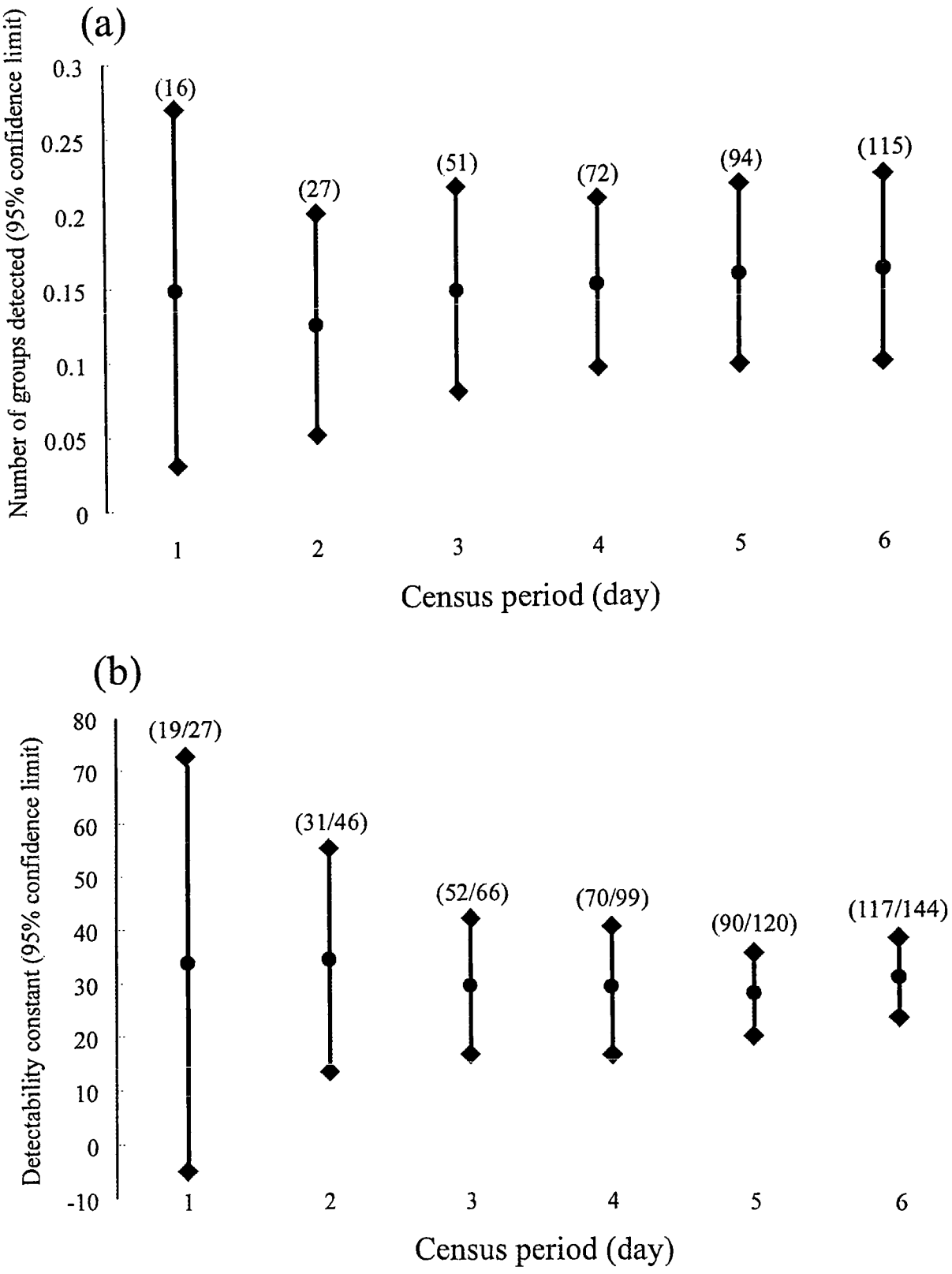

Fig. 3-4. Changes in 95% confidence limit of (a) the number of groups detected and (b) detectability constant ( ) with various durations of census day. In (a), only the 13 points sampled for the six entire days are used. Numbers in the parentheses indicate cumulative number of detection. In (b), numbers in parentheses indicate cumulative numbers of detections of followed groups/cumulative duration (hours) of group follows.

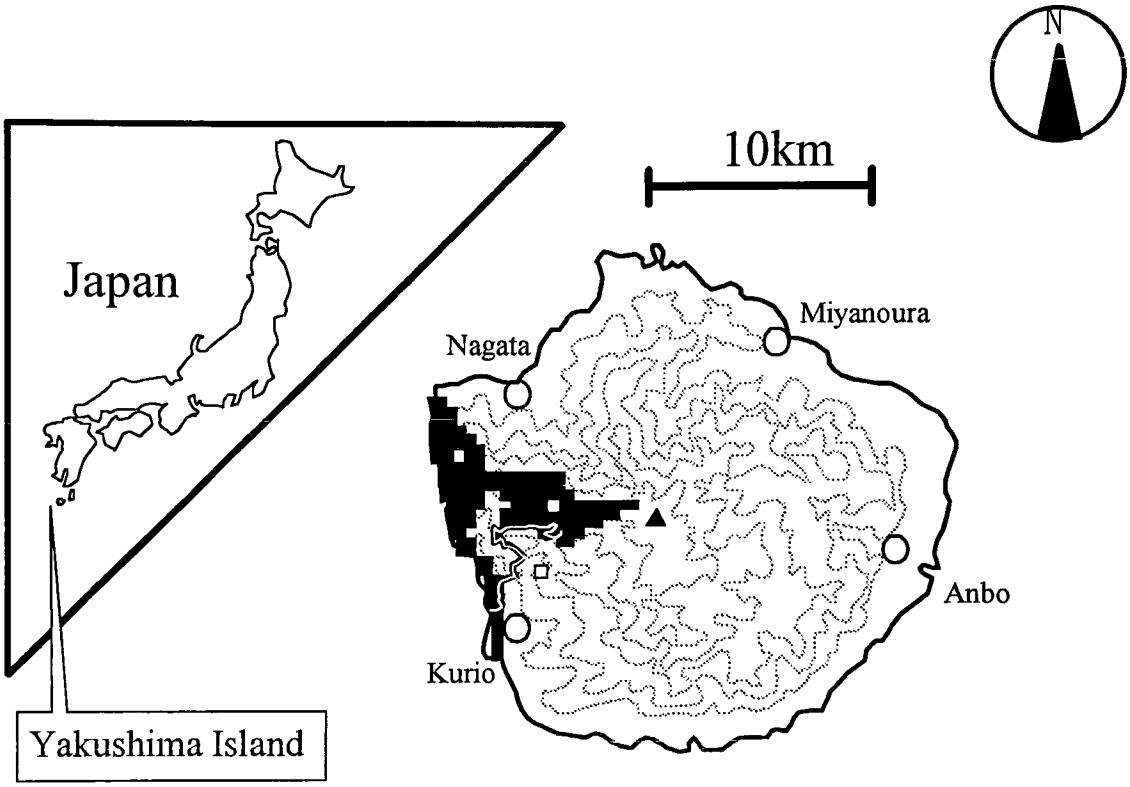

Fig. 4-1. Census area. Contours are drawn each 300m in altitude. Open squares indicate phenology plots. The filled triangle is the highest peak, Mt. Miyanoura (1,935m a.s.l.). Double line indicates a road along which number of food species was studied. Most of the faecal samples were collected on the road (chapter 5).

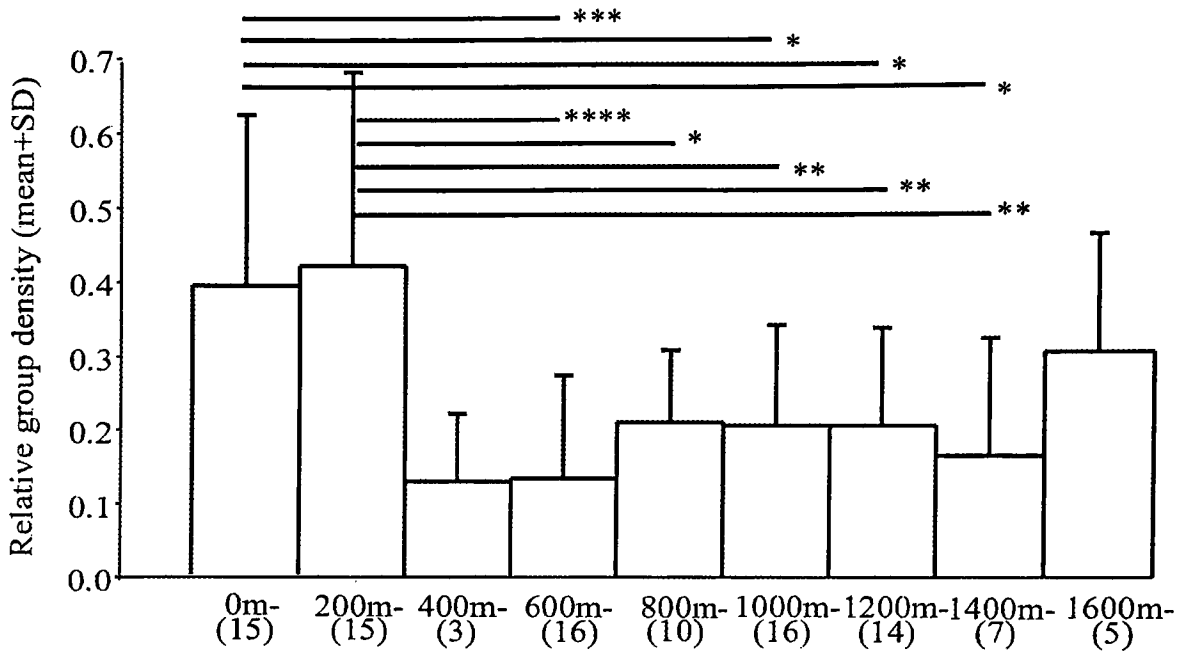

Fig. 4-2. Relative group density, or number of groups detected at observation points. Mean and standard deviations are shown. The difference was significant by Turkey-Kramer test between the zones connected by lines. * $p<0.1$, ** $p<0.05$, *** $p<0.01$, **** $p<0.001$.

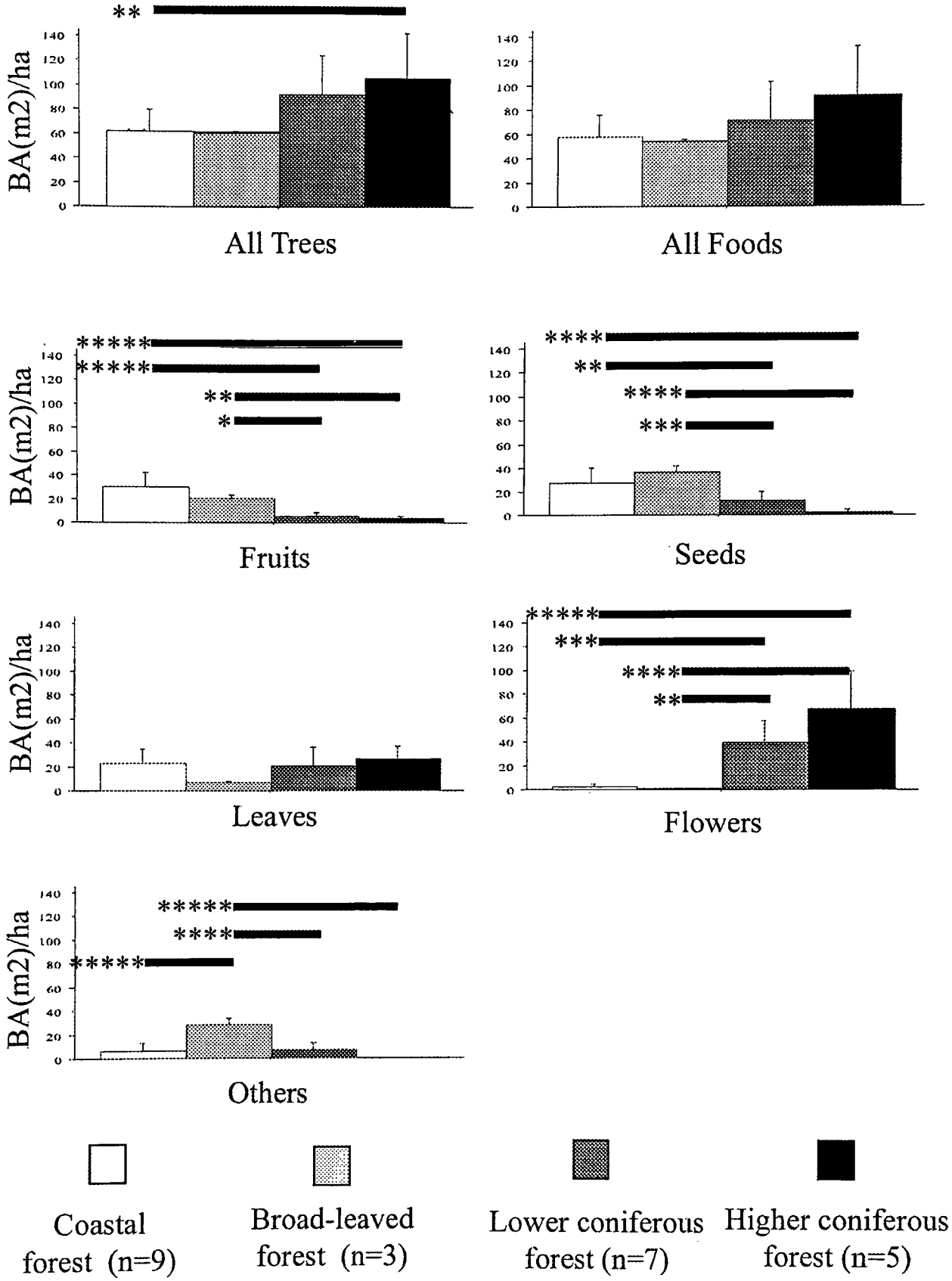

Fig. 4-3. Total basal area (TBA; m^2/ha) of food trees in the four altitudinal zones.

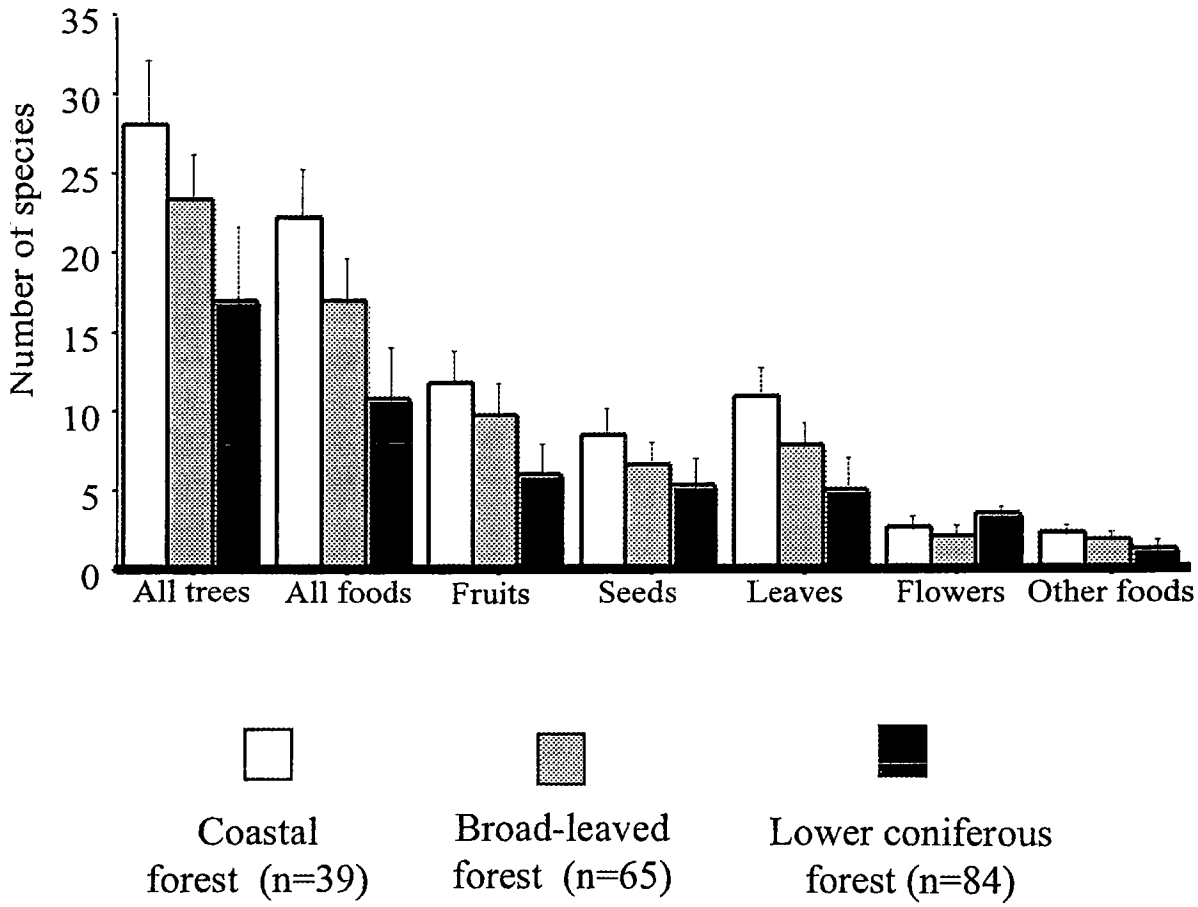

Fig. 4-4. Number of food tree species per unit area. Differences between zones were significant for all food categories by Turkey-Kramer test at $p<0.001$.

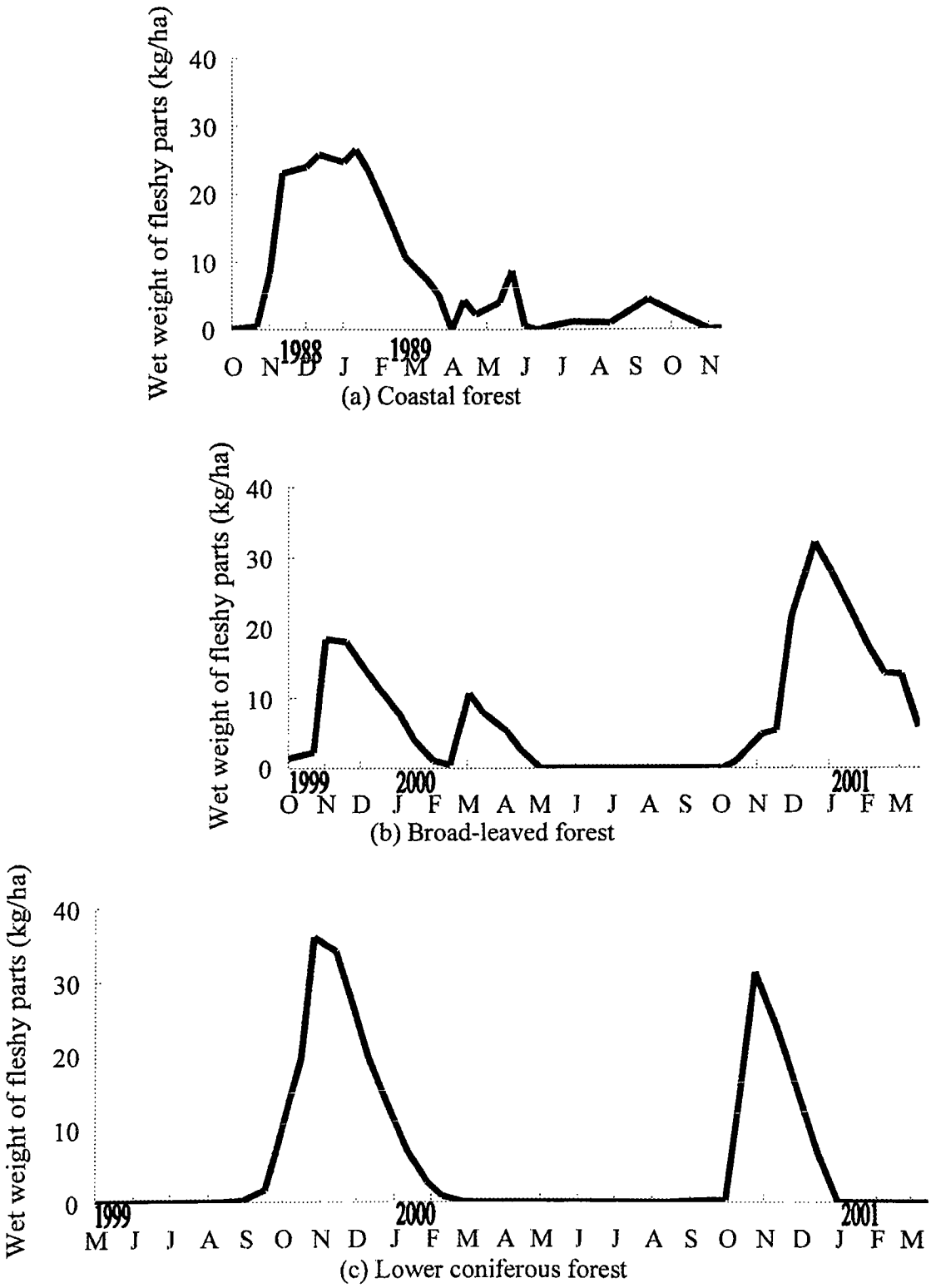

Fig. 4-5. Seasonal fruit abundance in the three altitudinal zones.

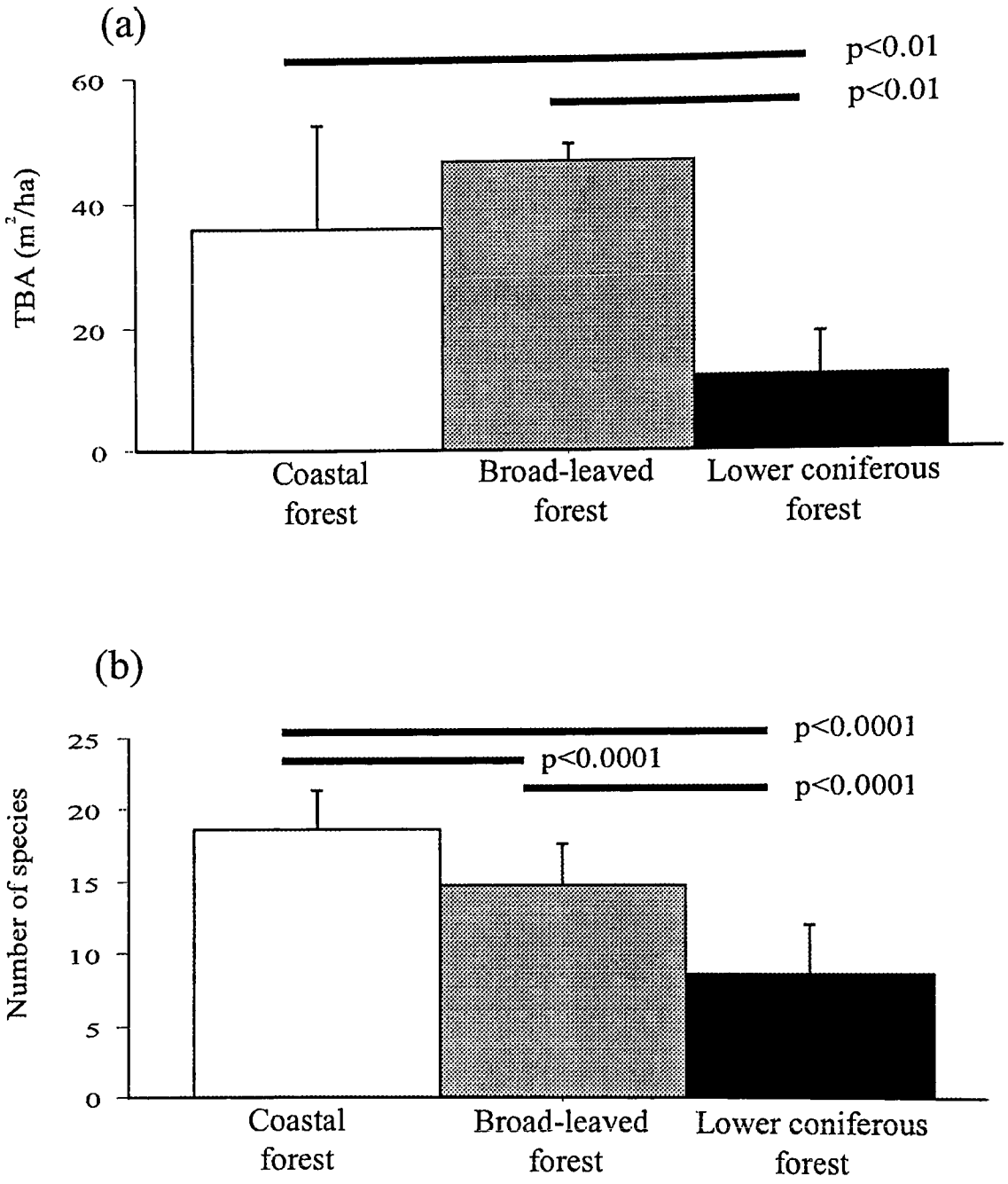

Fig. 5-1. Altitudinal comparisons of (a) basal area of seed/fruit-food trees among 19 plots and (b) number of seed/fruit species which appeared along a 100m-long segment of a road where faeces were collected. Means and standard deviations are shown. Food species were determined by the result of faecal analysis.

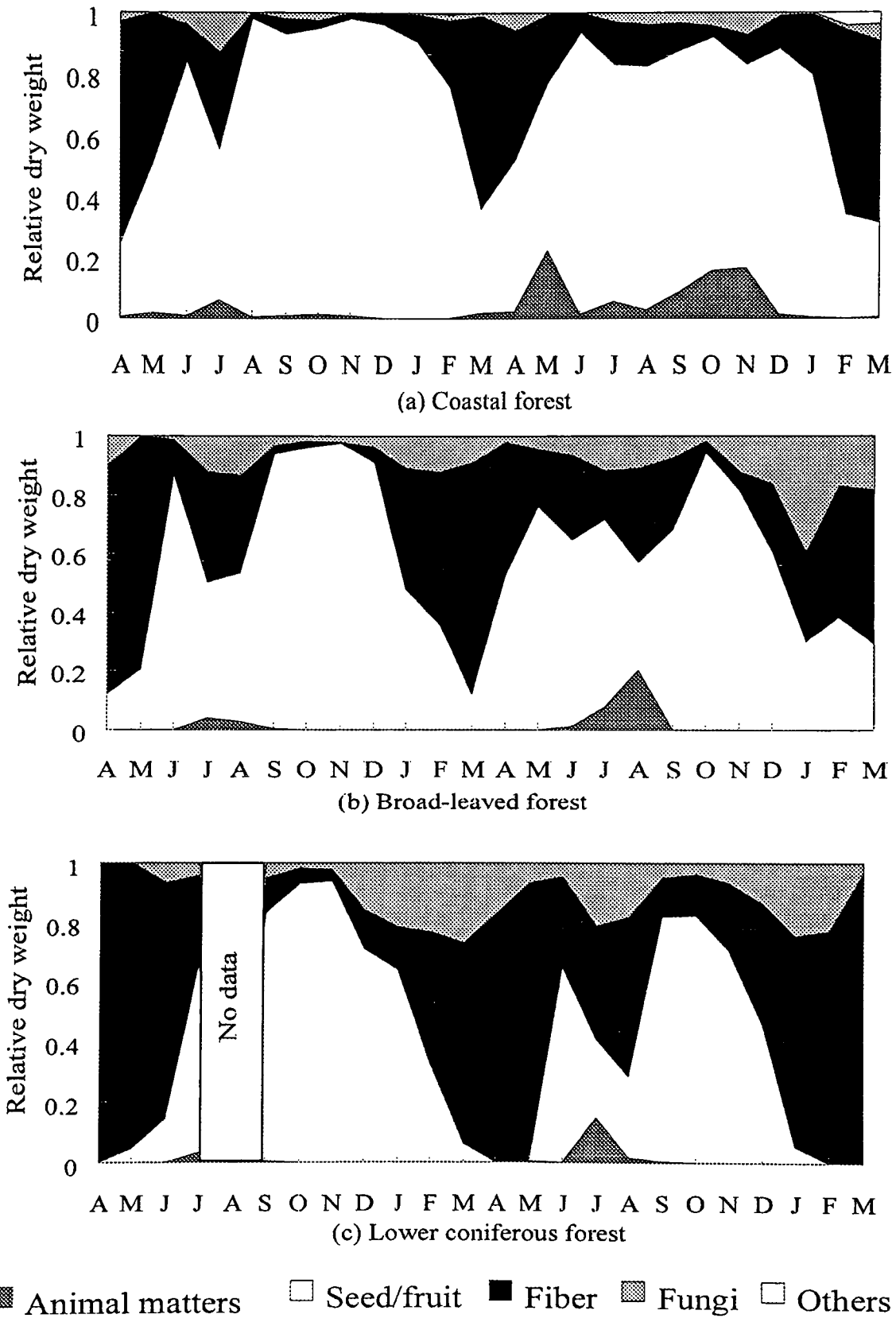

Fig. 5-2. Monthly changes of dietary composition in mean relative dry weight.

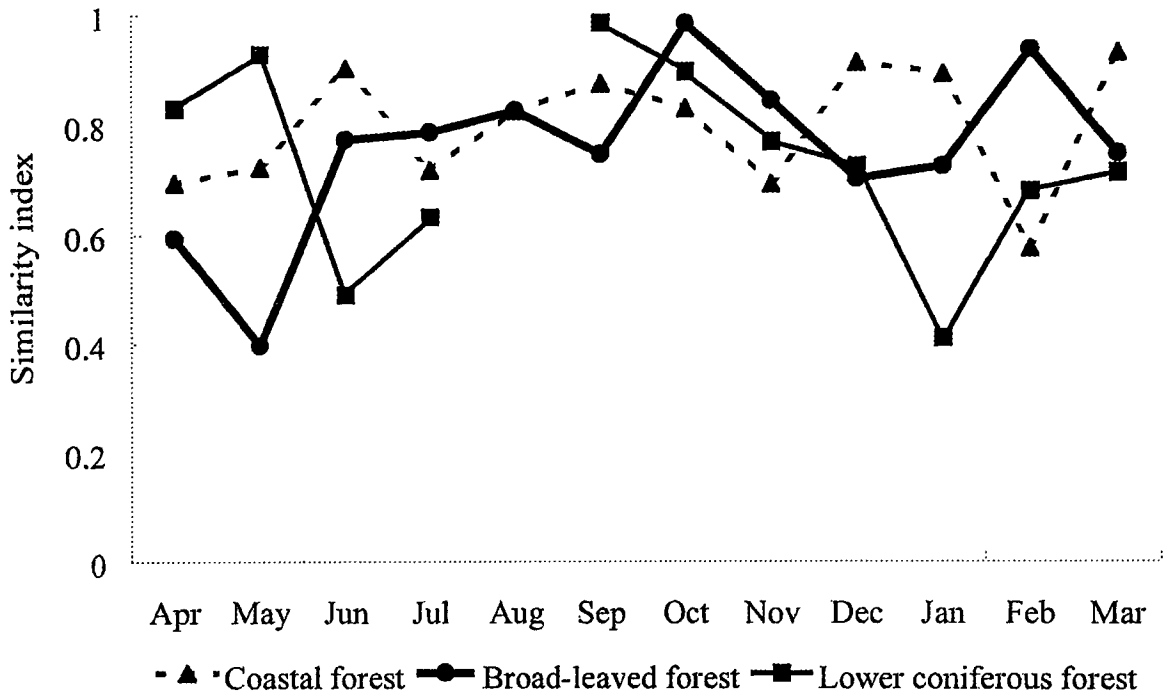

Fig. 5-3. Inter-annual variation of diet, expressed by similarity index between the same calendar month-pair.